VOLUME II MAY, 1933 No. 1

THE DISTRIBUTION OF BRITISH PURE-BRED FLOCKS OF SHEEP IN RELATION TO ENVIRONMENT[1]

BY J. E. NICHOLS.

(*Wool Industries Research Association.*)

(*With twelve Figures in the Text.*)

I. GENERAL INTRODUCTION.

THE history of sheep-breeding in each country is that of the rise and fall of various types of sheep, indigenous or introduced, in the continued conflict of altering environments, induced by new economic conditions, fresh demands for products and changing methods of land utilisation. From the point of view of the sheep-breeder, the limitations placed by local environment upon his choice of sheep variety and husbandry are made obvious by experience; but the questions of the distribution of sheep numbers and types in relation to habitat cannot be disregarded in the study of the origins of the supplies of sheep products.

Since the relationships of the various environmental factors (topography, climate, soil, etc.) to each other differ in each district and their effects cannot readily be dissociated, the proper emphasis to be laid upon any single factor cannot always be distinguished, except, for example, in the case of catastrophes such as drought and snow; further, the influences may affect either the quantitative or the qualitative distributions, in numbers per unit area, or in types, breeds or varieties of sheep. It is the latter which will be considered here.

Sheep are characteristically free-grazing animals, occupying the marginal areas in those countries with a temperate type of climate of the warmer variety. The ease of transport—and comparatively non-perishable nature—of wool assists the utilisation of extreme marginal areas with sparse human populations and large areas of land economically available (**7**); the better pasturages in the moister areas in lands in this category are favourable to the production of mutton and lamb. The dense centres of sheep distribution occur for the most part in areas with 20–40 in. annual rainfall (**2**).

The British Isles are included within the limits thus generally defined. From them have emanated the greater number of the breeds which have contributed to the sheep stocks of the major sheep-breeding countries; and there is much evidence that the numerous British breeds each require a certain optimal relationship of environmental factors for their successful propagation and maintenance.

The dependence of sheep type upon environment has been stressed frequently in accounts of British sheep but usually in rather general and vague

[1] Received for publication, June 26th, 1932.

terms; an exhaustive examination of the literature on this subject is not proposed, and mention will be made of only a few cases in which the effects of habitat are discussed. For instance, Low (**9**), in describing the local types in various districts, referred to the fact that the "Blackfaced Heath breed" was distributed in lands of cold, exposed climate, with vegetation of coarse heaths, mixed with sedges, rushes and inferior grasses, and ranged the greywacke hills of the South of Scotland; the Cheviot breed, on the other hand, fed more on grasses and inhabited a district of porphyry. Low also pointed out that the Penistone breed was limited in its distribution to the elevated district on the coal formation in Yorkshire, Lancashire and Derbyshire; the Southdown, better suited to dry and temperate than to cold and moist climates, had made most progress in breeding flocks on the chalk formation, while the old Longwool types were distributed most extensively in districts of new red sandstone in Yorkshire and the Midlands and on neighbouring areas of lias and oolite.

In the first half of the nineteenth century notable improvements in various breeds had been achieved and many local varieties had been influenced by the "new" Leicester and Southdown, but the spread of improved types had not obscured the limitations imposed by environment, indeed it apparently emphasised the differences in distribution between the basic forms. Brown (**3**) discussed fully the expansion of the Leicester and Southdown influences in relation to local environment, mapped the distribution of representative types in Great Britain and Ireland, and indicated the broad distinguishing features of the habitats of the main breeds. The effects of environmental factors upon particular characters have been commented upon by many; Cathcart (**4**), in a paper on "Wool in relation to science with practice," gave numerous references to previous discussions on the variation of wool characteristics under different natural conditions, and later, Heape (**6**) recognised the associations of different factors with differences in fertility in separate breeds. In recent years variations in the expression of certain characters have been related to external conditions (**1**, **5**, **10**, **11**, **16**); the distribution of sheep populations has been discussed by Johnson (**8**) and Huntington (**7**), and alterations in the estimated fleece weights in different districts with changes in distribution of sheep types have been examined (**12**).

In the majority of cases the reactions of type to environment have been studied with the aid of data from individual flocks in various localities or by relating the numbers of sheep (or density of sheep population) in given areas to the environmental conditions. Another method of approach to the general problem (similar to that employed by Brown) involves the study of the dispersion of the flocks of the distinct breeds in all localities in relation to the highest common environmental factors for each breed. If the pure-bred *flocks* are considered the changes in sheep *numbers* in any locality can be neglected to a large extent, and the confusions introduced by the movements of feeding

stock be avoided. On the other hand, the distribution of pure-bred flocks alone does not necessarily indicate the prevailing kind of sheep in point of numbers in all districts.

In the first place, except for certain "fancy" breeds such as the Piebald, the pure breeds found at the present time in the British Isles were always of local importance, selected to meet a local demand and to be compatible with local environment. With the development of new or improved types the suitability of these forms to other areas and for other purposes was tested, and in many cases the "breed" characteristics became altered in course of time as the type became established in its new locality (e.g. the North-country Cheviot), especially if the result of introduction were to displace more or less completely the original local form. Cross-breeding practices obviously affect the dispersion of pure-bred ram-producing flocks, and the suitability of a breed for this purpose in a particular district in conjunction with local supplies of breeding ewes may lead to the occurrence of "secondary concentrations" of pure-bred flocks in areas far removed from the primary concentrations in the regions of their development (e.g. the Down flocks in the Tweed valley in relation to the Cheviot and half-bred ewe flocks of the neighbouring hills).

Aggregations of pure-bred *flocks* of a breed may indicate either successful survival of that type in response to local demands or a change in type or demand under local conditions—in either case their distribution may be utilised as a means of approach to the question of type and habitat. It must be re-emphasised that owing to the numerical predominance of cross-bred stock in most districts with the exceptions discussed below, density of sheep population is not considered here.

In 1928 a large-scale map of the British Isles was prepared; on it the position of each pure-bred flock was indicated as closely as possible and small-scale reproductions showing the aggregations of the flocks of the majority of the breeds have been made. A short account of the breed distributions has previously been given (**13**) together with the map of the chief mountain varieties which is reproduced herewith as Fig. 1; Figs. 2 and 3 show the geographical positions of concentrations of other types. The conditions under which the breeds exist may be described by considering either each breed in turn in relation to the environmental factors which may be defined, or the various situations in respect of each factor for the several breeds. The latter does not so readily allow the interrelation of the direct or indirect effects of the numerous factors but is adopted at present so that the conditions may be segregated without reference to their influences on each other or on all the circumstances which attend sheep husbandry.

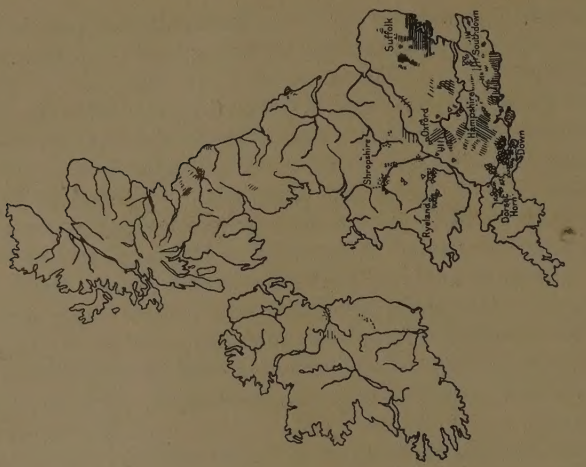


Fig. 3

Fig. 2.

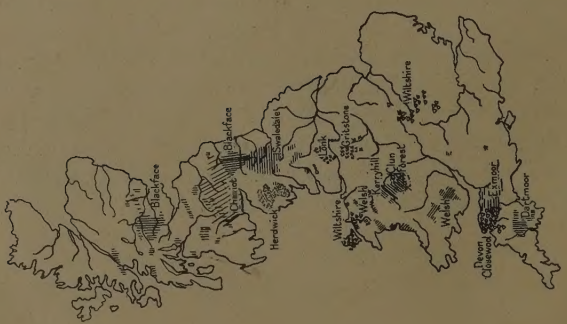


Fig. 1.

II. ALTITUDE—AREA.

From the large-scale map of flock distributions, estimates were made of the areas in which the aggregations of the flocks of each breed occurred—these of necessity are only rough approximations, especially in the cases of such breeds as the Oxford and Shropshire, with no intense concentrations. The altitude range throughout which the flocks are found was observed and the two series of conditions are shown in combination in Fig. 4, in which the base lines

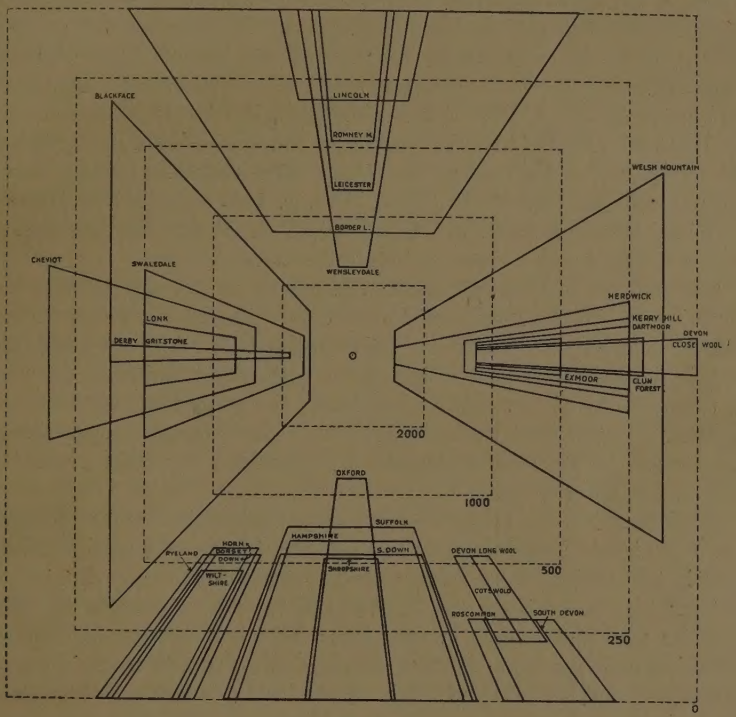


Fig. 4.

indicate the areas covered (scale 1 cm. = 950 sq. miles approximately) and the depths of the cones the dispersions in respect of altitude. Thus pure-bred Oxford flocks are for the most part distributed over an area of about 1140 sq. miles and at all heights from sea level to about 1250 ft.

Among the Down types, the Southdown, Hampshire and Suffolk are closely similar in area range (3200–3600 sq. miles) and differ only to about 100 ft. in altitude range, some of the Scottish secondary concentrations of the Suffolk contributing to its dispersion to just over 800 ft. These breeds have retained their predominance as pure-bred types in the regions of their

development or in closely adjacent areas and the Suffolk and Hampshire have also been adopted for crossing purposes in the Midlands, the former having further secondary concentrations in Ireland (Meath and West Meath particularly), in the south of Scotland (Berwickshire) and in Northumberland. Shropshire and Oxford flocks are largely confined to their name and near-by counties, but the vertical distribution of the latter has been increased by the secondary aggregations in Berwickshire and East Lothian where ram production is the chief function of the pure-bred Down flocks. Dorset Horn and Dorset Down flocks are concentrated in Dorset and Somerset and, except for isolated flocks, have spread little, although the Isle of Wight includes a secondary concentration of the former breed. The Ryeland shows aggregations not only in Hereford, Brecon and Monmouth, but has invaded Southdown and Hampshire Down territories with minor concentrations in Kent, Berkshire and Hampshire, and several flocks in Gloucestershire, until its area distribution has exceeded that of the Dorset Horn (*c.* 1100 sq. miles) by about 300 sq. miles. Wiltshire flocks are found chiefly in Bucks, Northampton and Anglesey, with a minor concentration in the Conway valley.

The counties of Cornwall and Devon possess all the aggregations of the South Devon, Devon Longwool, Devon Closewool and Dartmoor, while the Exmoor is largely confined to its native uplands. These breeds differ chiefly in their altitude dispersions, which appear particularly well defined for each; for example, the 300 ft. contour line marks the upper limit of the range of situation of South Devon pure-bred flocks, while the great concentrations of Exmoor and Dartmoor lie above 500 ft., although a few flocks of the latter are found at lower levels.

The Longwools as a group illustrate several important features of distribution. The Lincoln, Romney Marsh and Leicester breeds are essentially lowland types in that their pure-bred flocks are distributed from sea level to less than 1000 ft.; they are limited also in area and form a contrast to the Border Leicester and Wensleydale in that these have been developed largely for producing rams for cross-breeding purposes in relation to mountain breeds. In Scotland and the north of England, Border Leicester flocks are found in the lowlands and valleys more or less fringing the Blackface and Cheviot districts, the extensive breeding areas of these mountain types leading to numerous local concentrations of the Border Leicester ram-breeding flocks; there are also one large and several minor secondary aggregations in Northern Ireland. Wensleydale ram-breeding flocks are similarly associated with the Swaledale type with secondaries in Furness (towards the Herdwick breeding areas), the Lune valley and in proximity to the Lonk breeding areas in Lancashire. The altitude and area ranges of these Longwools are extended in their specific applications to the mountain ewe stocks.

In lowland areas the distribution of pure-bred flocks does not give a picture of the sheep population in numbers according to type as the great

majority of breeding and feeding stock is cross-bred—on the other hand, in more elevated districts the type of the mountain pure-bred flocks predominates in the commercial breeding flocks. In many instances, such as the Scotch Blackface and Welsh Mountain, the registered flocks are chiefly those which are specially organised for ram-breeding; they tend in all breeds to be maintained in regions with less severe environmental conditions. In these breeds, therefore, the distributions shown tend to be marginal to the commercial flocks existing at higher altitudes, circumscribing the aggregations of the latter, and to be more limited in area; but in other mountain types, e.g. Swaledale and Herdwick, the distribution of registered flocks closely coincides with that of the breeds as a whole. In the maps the strict limitations of many of the mountain breeds are clearly shown, and also the succession of types along the Pennines from the Tyne Gap to the Peak District. Fig. 4 indicates that the chief distinction which can be made in respect of altitude range between mountain and lowland types in the British Isles is that the latter have generally an upper limit of 1000 ft. while the former can range to greater heights.

Owing to the numerous forms of husbandry and economic situations found within the British Isles, there is great local competition among the breeds. In continuous highland areas considerations of altitude alone would not appear sufficient to define the distribution of sheep types—other limiting factors will be examined later. Similarly in the lowland breeds, other conditions influence dispersion, one of these being suitability for crossing purposes. In this respect the wide distribution of the Border Leicester may be considered, for the moment, as being due to its adaptability for crossing with several mountain types, while the Wensleydale is more limited, chiefly to the Swaledale; and the former can serve, in addition, as an ewe-producing type, e.g. in the Irish Free State, on low country. At the same time this factor in dispersion cannot apparently override other influences; as, for instance, in the case of many of the Down breeds which are popular for cross-breeding, but have not spread so widely that they exhibit aggregations in or near the primary breeding areas of the ewe stocks with which they are crossed.

III. TEMPERATURE—RAINFALL.

The most profound effects of climatic factors must of necessity be indirect in their action upon food supply, types of farming, etc.; in certain cases, however, weather may exert obvious direct influences. In so far as sheep types are maintained in association with certain forms of husbandry, they exhibit varying relationships to major climatic conditions, and unusual climatic effects in some seasons may, by their action on nutrition supply, cause material changes in the numbers of sheep in some districts, e.g. failure of root crops in summer and autumn may interfere with the usual movements of bought stock into a fattening district. Similarly, the expression of disease effects

may be influenced by climatic conditions, e.g. fluke and foot-rot, although essentially the effects can only be manifested within the environments of the causal organisms—in themselves an ecological study.

In the case of pure-bred flocks, especially of the lowland breeds, however, such actions of climatic and other influences are comparatively unimportant, in a normal course of seasons, except in relation to flock numbers. At the same time direct effects may be produced by these environmental factors, in highland flocks in particular, as through increased early mortality in cold, wet weather, which in the long run may require adjustment of the time of lambing to a period at which untoward weather may be less expected. Further, there is some evidence that the onset of the mating season may be partially influenced by meteorological factors (**11**). These two periods, service and lambing, together with the time of change of dentition, may be considered critical to the existence of the sheep stock, especially in respect of susceptibility to direct as well as indirect environmental effects. The last attains great practical importance in certain overseas countries (e.g. parts of New Zealand), while an additional critical period occurs at weaning time, which may cause particular concern in parts of Australia and in Kenya, where in many flocks the time of lambing has to be arranged so that weaning takes place when good weather and succulent herbage obtain. (The requisite displacement of the normal breeding season can be accomplished more readily with the Merino than with British breeds.) These considerations accentuate the statement that the distribution of rainfall throughout the year is generally much more important than the total annual rainfall, especially in regions where the evaporation is great. (Summarised data for the numbers of rainy days per month have been given previously (**14**).)

In the accompanying diagrams the temperature and rainfall conditions are shown jointly after the hythergraph method of Taylor (**15**); this method was also employed by Johnson (**8**) in his studies of the distribution of sheep populations. The data have been obtained from *The Book of Normals of Meteorological Elements for the British Isles, for periods ending* 1915 (Air Ministry, Meteorological Office, 1919). The points on the inner, broken lines in the figures are the monthly means, for the period 1881–1915, for all stations which fall within (or in close proximity to) the aggregations of the various breeds as determined from the large-scale map of flock distributions. The outer, solid line circumscribes all the extreme points of the monthly means for the stations for the 35-year period.

Thus the figures formed by the broken lines represent the mean hythergraphs for the breeds, while the solid line figures include all monthly means of temperature and rainfall. The latter do not indicate the *extreme* conditions recorded for these meteorological elements, but may be used to illustrate the ranges of monthly means which have obtained during the period; in the discussion these figures are referred to as "inclusive" graphs. The spatial

difference between the two graphs for each breed (except in, e.g., Dorset Down and Cotswold, where records from only one station could be used for each breed) is due to the number of stations and/or the range of monthly means; in any case, it may give some indication of the plasticity of the breed in respect of climate or area. (The numbers of stations considered for each breed are given in brackets after the breed name; these are actually small, and without evidence as to the "permanence" of certain flocks, too close consideration of the spatial differences in the graphs as indices of breed plasticities must not be made.)

Stations with similar climates may contribute to the figures for different breeds, and some are common to several breeds; these situations can also be viewed as evidence of breed plasticities in the same sense. (It is recognised that relative humidity may be one of the chief climatic factors involved, and the relevant data can be associated with temperature figures in climographs as in the hythergraphs discussed below. Such records are apparently not available for periods or stations allowing their specific treatment in relation to the breed distributions.)

The Downs are closely similar in their mean hythergraphs, except the Dorset Down with its wetter autumn and winter months; the greater variations exist in regard to the inclusive graphs, especially in the case of the Suffolk, Hampshire and Oxford. The mean figures for Southdown and Hampshire fit closely, but the latter undergoes much wetter conditions in October–December than the former, as shown by the inclusive graphs. The Hampshire graphs record heavier rainfall than the Suffolk for most of the year. The mean figures for Oxford, Suffolk and Shropshire are also fairly similar, but their inclusive graphs differ rather widely in form. The Hampshire and Southdown are alike in area distribution (Fig. 4) but not in their inclusive figures; the Hampshire and Oxford have distinct area and altitude distributions but show much similarity in these meteorological conditions.

The Dorset Horn, Dorset Down, Ryeland and Wiltshire, which are fairly alike in area and altitude, exhibit marked differences in their relationships with temperature and rainfall. The breeds in Devon and Cornwall show distinctive graphs, the contrast in altitude between South Devon and Devon Longwool, previously noted, being emphasised by the climatic factors.

The Kerry Hill and Clun Forest breeds show close geographical proximity in their aggregations (Fig. 1), minor differences in altitude range, but relatively great ones in area; the conditions of temperature and rainfall, however, for the latter breed are completely included in those for the former with its wide spatial difference between inclusive and mean graphs.

In the Longwools, the Leicester and Lincoln contrast with the Border Leicester and Wensleydale; each pair of breeds is similar in mean hythergraphs and in the general form of inclusive graphs. The extension in the direction of heavier rainfall in August–December for the Wensleydale is

contributed by one station (Stonyhurst), and this is also shown for the Swaledale breed.

The Cotswold and Romney Marsh, though localised breeds as are the Lincoln and Leicester, show distinctive features of the hythergraphs in the wetter winter conditions. The plasticity in this direction in the case of the Romney may be of importance in relation to its distribution in other countries (see below).

In the mountain breeds the figures are not representative to the same extent in all cases, for the reasons discussed above in connection with the distribution of registered flocks, but the differences in the relationships of temperature and rainfall are peculiarly well marked, especially when the succession of mountain types from north to south in Great Britain and the altitude-area ranges of the breeds are considered.

The alternation of relatively wet and dry months from July to January over most of Great Britain is clearly shown in the figures, with the general tendency of comparatively great falls in temperature in the monthly means of September to November. In this respect there may appear to be indications from these graphs of the relative times in the year of the critical periods of service and lambing for various breeds; but the relationships may be spurious. In the various breeding districts the time of service is usually well established by practicability and custom. In the figures, the months in which the temperature is tending to rise after its minimum and the rainfall is lowest appear to be those when lambing is customary. It might be suggested that the nearest approaches of the mean hythergraph to the arbitrary point of 40° F. and 2 in. rainfall are the lambing months. In most graphs these correspond to a time of service in autumn when the mean monthly temperature has begun to fall, before the late autumn and winter monthly rainfall has approached its maximum.

For purposes of comparison with the relationships of temperature and rainfall found in Great Britain, a number of hythergraphs have been drawn for stations in Australia, New Zealand and the Irish Free State. These also serve to indicate a possible application of this aspect of breed distribution to questions of the most favourable habitats for the breeds in other countries; but in this respect the hythergraphs can only be considered as one criterion of the general similarity in the agricultural situations in the home of the breed and elsewhere, while the factors considered may not necessarily have the same relative values or potentialities in different regions. For instance, in Australia in districts with low rainfall and high temperatures, e.g. Bourke and Broken Hill, considerations of evaporation may thoroughly disturb any effects of temperature-rainfall relations. Moreover, methods of husbandry can reduce the influences of climatic factors; shade and shearing may counteract effects of high temperatures, and the provision of water supply or succulent fodder such as lucerne or young cereal crops may help to overcome natural deficiencies

in the available grasses in districts with warm springs, hot summers and low rainfall.

In connection with the Australian stations (the data being obtained from Official Yearbooks and Statistical Reports), discussion will be confined to few of the British breeds, but it will indicate the general principles which can possibly be applied in this aspect of the study.

If the Hampshire be taken as the most plastic of the Downs in respect of these meteorological elements it is apparent that Sydney is unsuitable, for only in spring (August and September) do its temperature-rainfall conditions fall within the inclusive graph of the Hampshire. For Bathurst, Goulburn and Wagga Wagga, the period April–May to October–November lies within the Hampshire figure though towards the drier parts, and the rest of the year has higher temperatures; for Melbourne, conditions from April to November occur close to the mean hythergraph for this breed, while for Hobart only the January, February and March points are outside the inclusive figure. From April to December at this station, temperature and rainfall conditions would appear to be closely approximated to the means for the Southdown and Shropshire breeds. At Adelaide, from April–May to September–October, the conditions fall within the Hampshire inclusive figure, the rainfall during the rest of the year being too light and contributing relatively more to the divergency of the two figures.

If the Dorset Horn breed be considered, for Hobart only the February temperature falls outside the inclusive graph, from April to December conditions being near or inside the mean; for Adelaide, from October to April, they are outside the inclusive figure (especially in respect of rainfall from March to November), but the similar general inclination of the graphs (the long axes of the figures being roughly parallel) may have some significance.

The inclusive graphs for the Leicester and Lincoln breeds cover also the conditions from April to November at Bathurst and Goulburn, April to October at Melbourne, and March–April to November–December at Hobart; for the Romney only February at Hobart has temperature-rainfall outside its inclusive figure and November to March at Melbourne. In the latter case the low rainfall for January and February is the greater distinguishing feature, which is also the situation when the figures for the Border Leicester are used in comparison. For this breed, the temperature conditions from December to March at Hobart and from November to April at Melbourne extend the graphs of these stations beyond its inclusive figure.

In further illustration the South Devon may be used as an example of a breed which in Great Britain is definitely localised but which exhibits widely dispersed mean and inclusive figures. The latter overlaps the Sydney hythergraph in June to September, the Goulburn and Bathurst graphs only for September to November and September to October respectively, while Hobart and Melbourne conditions lie beyond the inclusive graph for this breed from

December to March, in July and also, for the former station, in August. It will have been noted in the foregoing discussion that the stations considered are chiefly those which are situated in or near lands which have been developed for agricultural practices including maintenance of British types of sheep or their crosses with the basic Merino.

In New Zealand as a whole the environment for the breeds approaches more closely that of Great Britain than it does in Australia, but there is much variation between localities especially in respect of climate and altitude. So far as the factors here considered are concerned, it is possible to estimate roughly the expectations of the suitability of conditions at New Zealand stations for the British breeds. In Table I, where the hythergraph for the station approaches that of the breed mean, it is indicated by +++; if it is circumscribed by the inclusive breed graph by ++; where more than half lies within the inclusive figure by +, more than half outside by −, and where there is no overlapping of the figures by −−. Intermediate relationships are shown, e.g. ++1 indicates that the station hythergraph is included and approaches the mean for the most part; when it is outside for six months +− is used.

Table I. *Expected suitability of climatic conditions for British breeds of sheep at New Zealand stations.*

Breed	Dunedin	Queenstown	Invercargill	Hammer	Nelson	Lincoln	Auckland	Tauranga	Rotorua	Napier	Wellington	New Plymouth
Southdown, Shropshire	+	++	−	−	−	+++	−−	−−	−−	+	−	−−
Suffolk	+	++	−	+	+−	+++	−−	−−	−−	+−	−	−−
Hampshire, Oxford	++	+++	+	+1	+	++1	−−	−−	−−	+	+	−−
Dorset Horn	++1	+++	−	+	+	++1	−−	−−	−−	+	+1	−−
Ryeland	++1	++1	++	+1	+	++	+−	−	+	+	+1	−−
Leicester, Lincoln	+−	+1	−−	−	−	+1	−−	−−	−−	−	−	−−
Romney	−	++1	−	−	−	+++	−−	−−	−−	1−	−	−−
Border Leicester	++1	+1	+1	+1	+1	+1	−−	−−	−−	+1	+	−−
Wensleydale	+−+	+1	+−	+1	+1	+	−	−	−	−	+	−−

Thus for the Southdown, Shropshire and Suffolk breeds it might be expected from these climatic data that Lincoln (in Canterbury) would be the most suitable district (other things being equal) with Queenstown, Dunedin in the South Island and Napier in the North Island less suitable. Among the Longwools the Border Leicester might find a climatically favourable environment in the six South Island stations and at Napier and Wellington with Dunedin apparently the most favourable. For the breeds shown, the South Canterbury district (as exemplified by the Lincoln station) would appear to exhibit the most generally suitable conditions, followed by Queenstown. In practice, however, the situation, altitude and topography of the Queenstown area tend to override its apparent advantages of temperature and rainfall.

SHROPSHIRE (4)
SUFFOLK (8)
SOUTHDOWN (5)
DORSET DOWN (1)
OXFORD (8)
HAMPSHIRE (10)
60
50
40
30
2
3
4
5

Fig. 5.

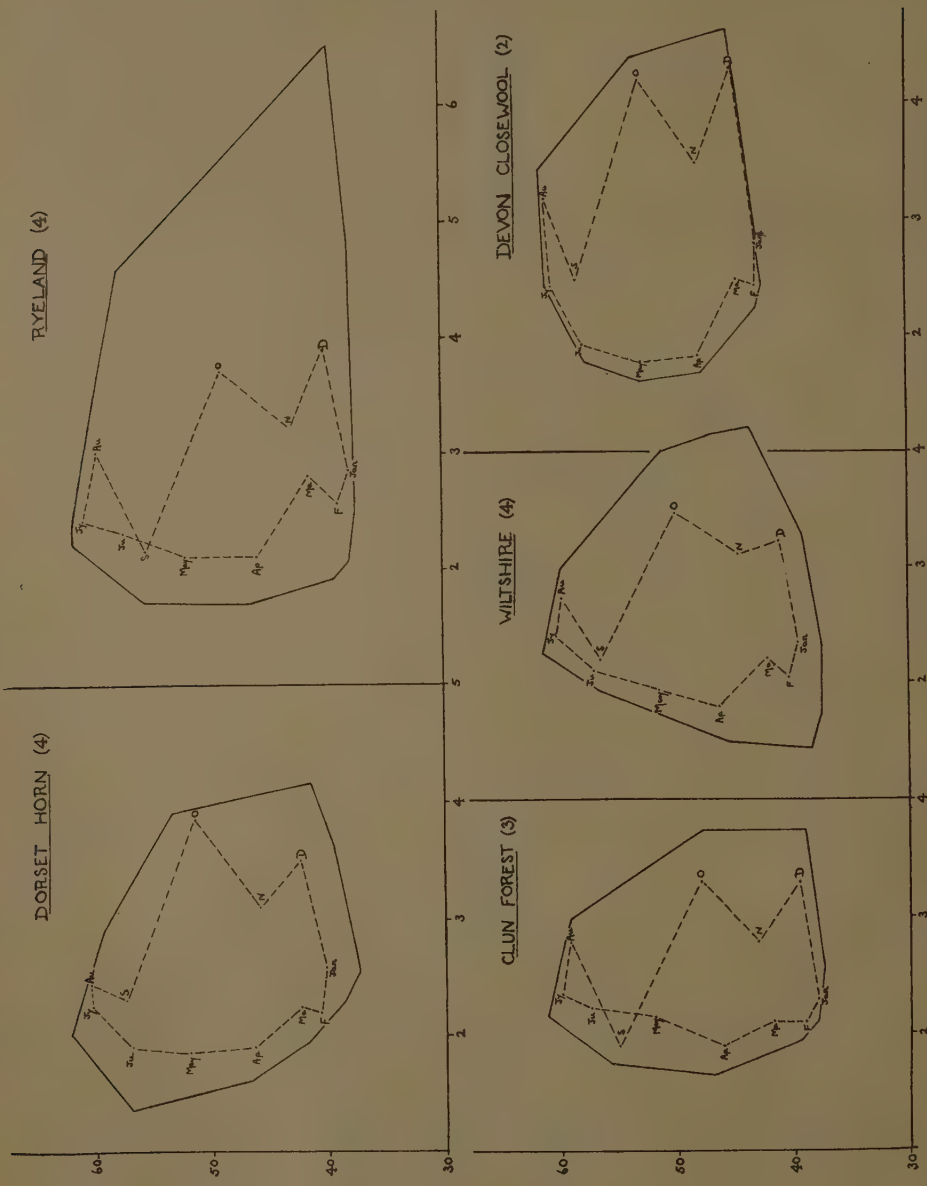

RYELAND (4)
DEVON CLOSEWOOL (2)
DORSET HORN (4)
WILTSHIRE (4)
CLUN FOREST (3)
60
50
40
30
6
5
4
3
2

Fig. 6.

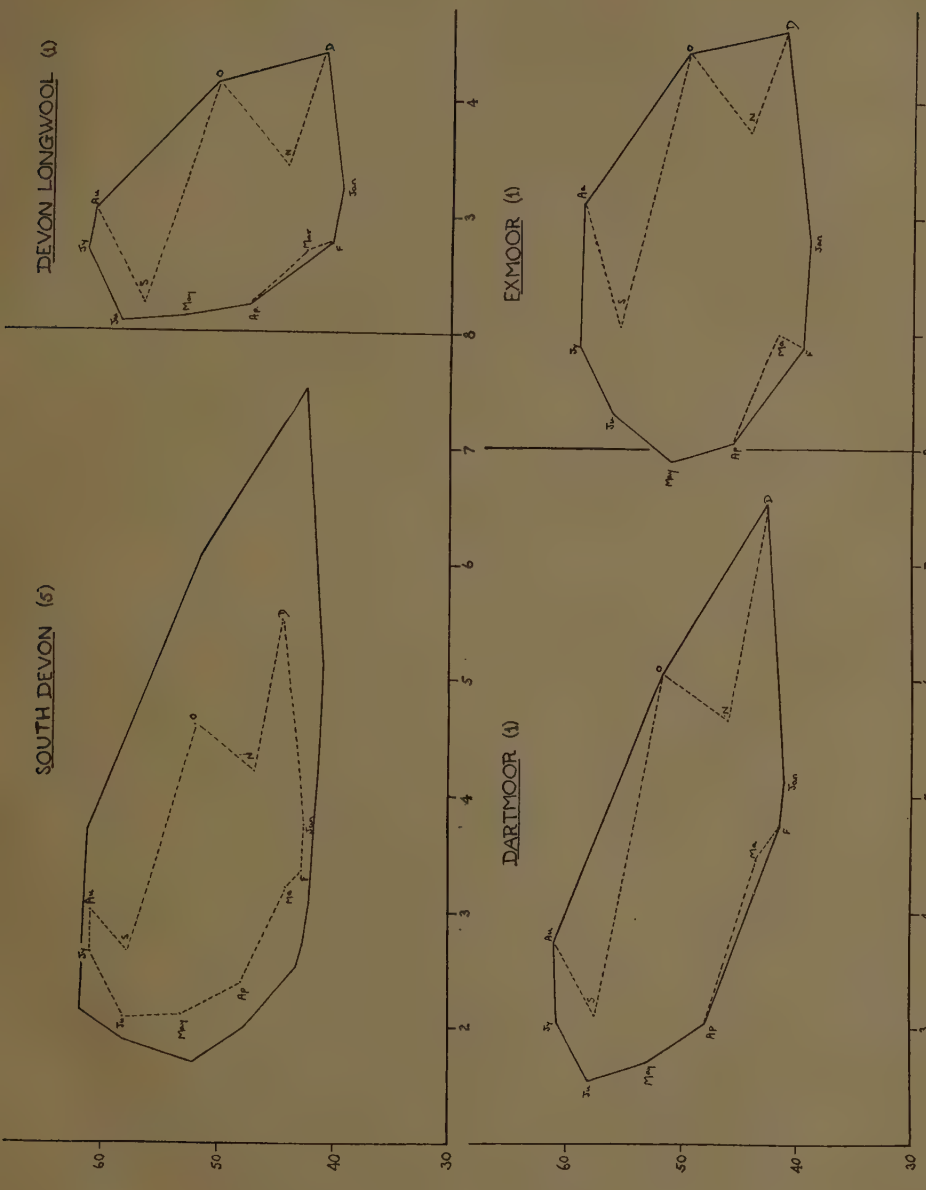

DEVON LONGWOOL (1)
SOUTH DEVON (5)
EXMOOR (1)
DARTMOOR (1)
60
50
40
30
2
3
4
5
6
7
8

Fig. 7.

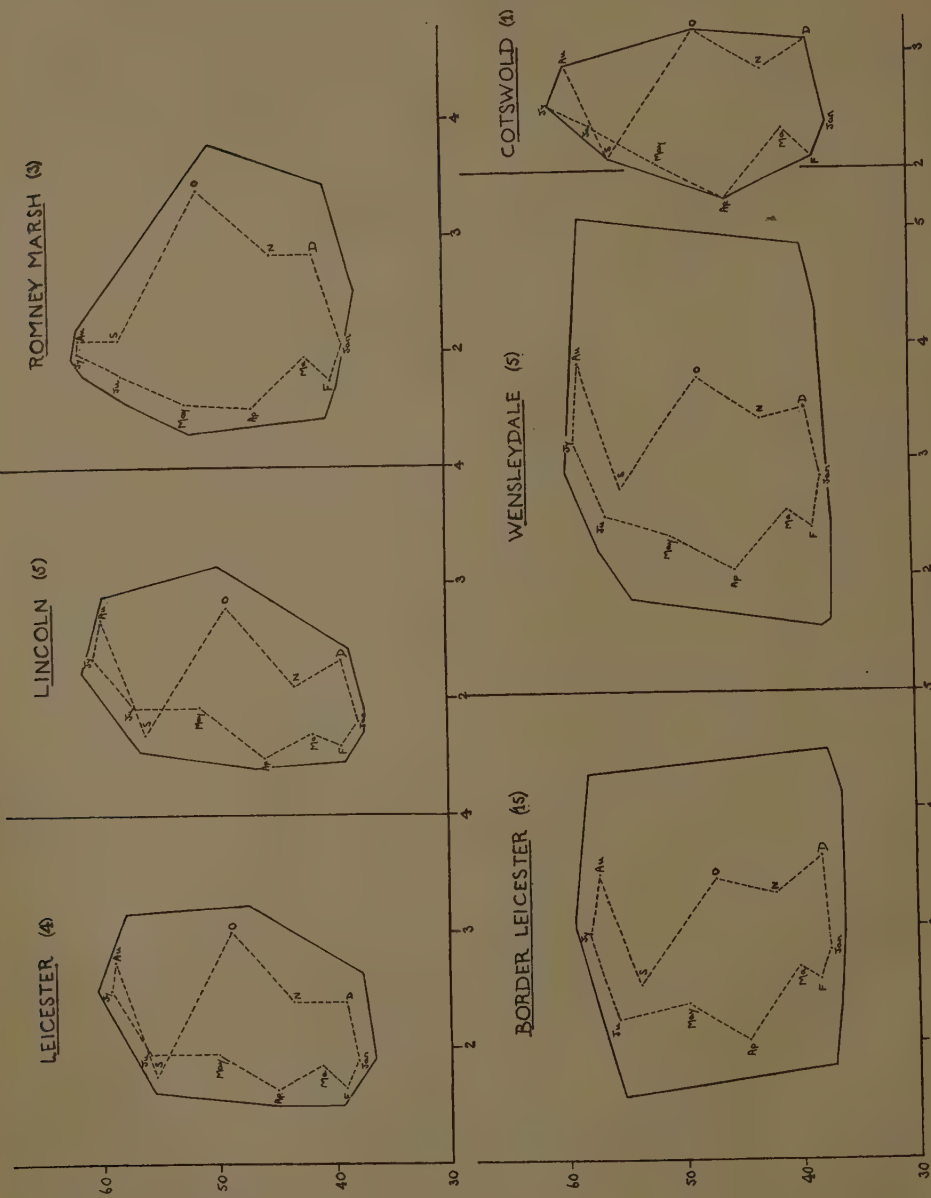

ROMNEY MARSH (3)
LINCOLN (5)
LEICESTER (4)
COTSWOLD (1)
WENSLEYDALE (5)
BORDER LEICESTER (15)
60
50
40
30
4
3
2
5

Fig. 8.

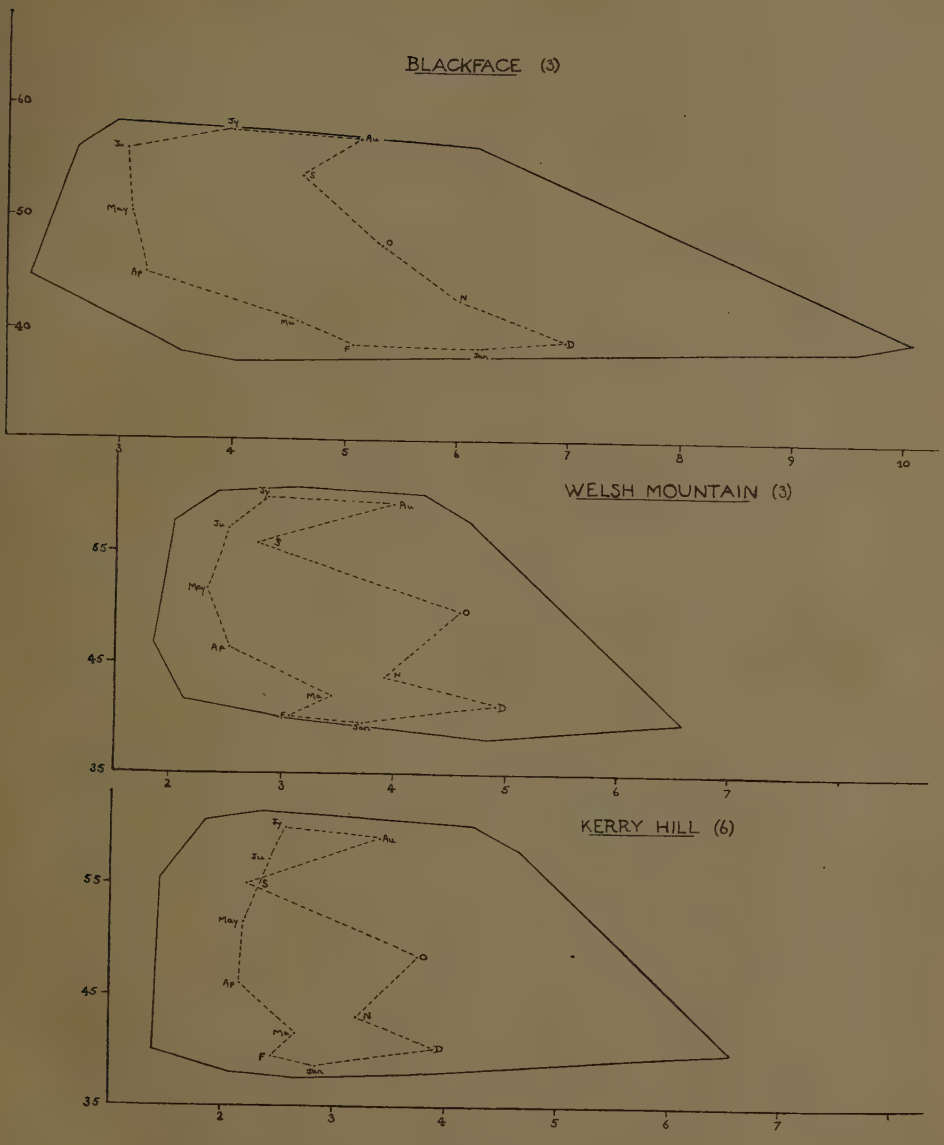

BLACKFACE (3)
60
50
40
Jy
Au
Ju
S
May
O
Ap
N
Mr
D
F
Jan
3
4
5
6
7
8
9
10
WELSH MOUNTAIN (3)
55
45
35
2
3
4
5
6
7
KERRY HILL (6)
55
45
35
2
3
4
5
6
7

Fig. 9.

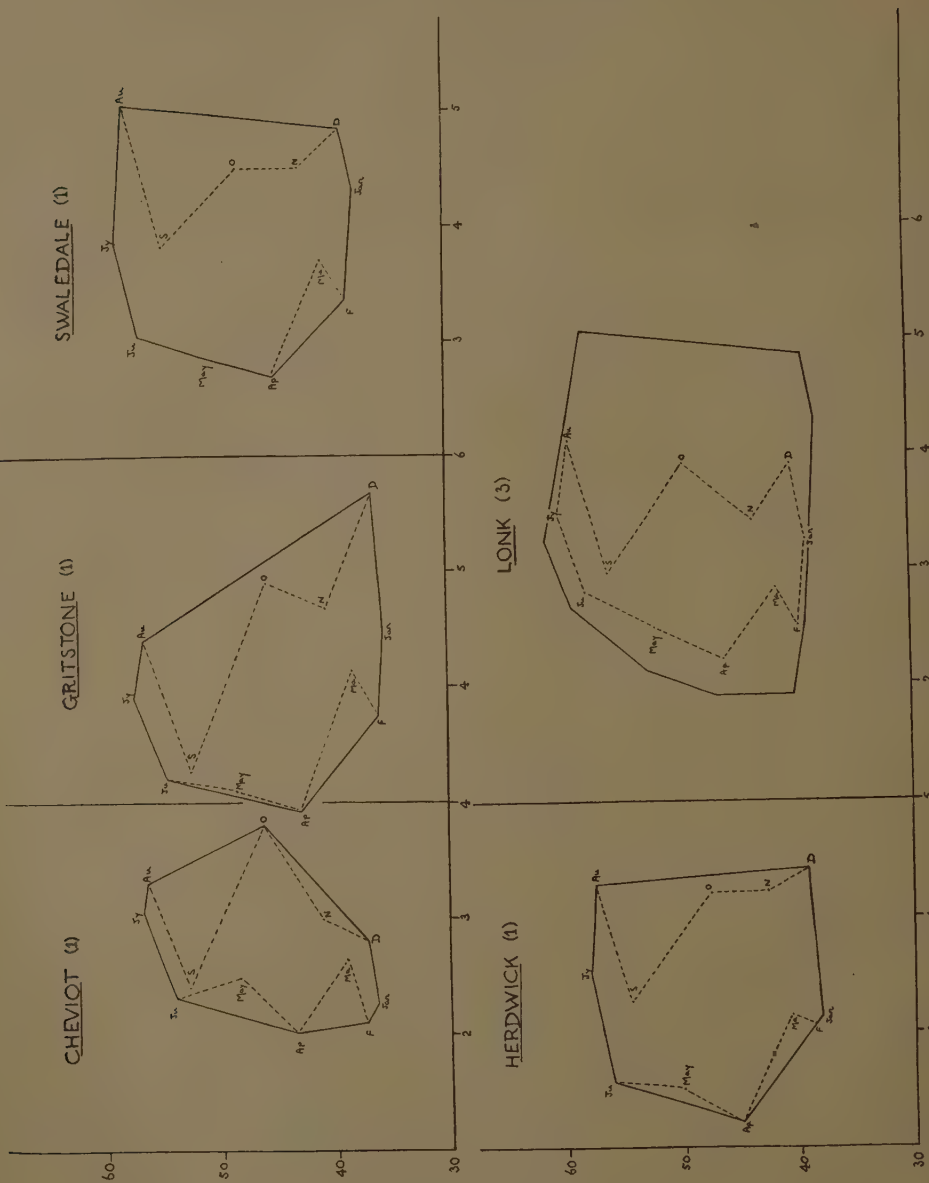

SWALEDALE (1)
GRITSTONE (1)
LONK (3)
CHEVIOT (1)
HERDWICK (1)
60
50
40
30

Fig. 10.

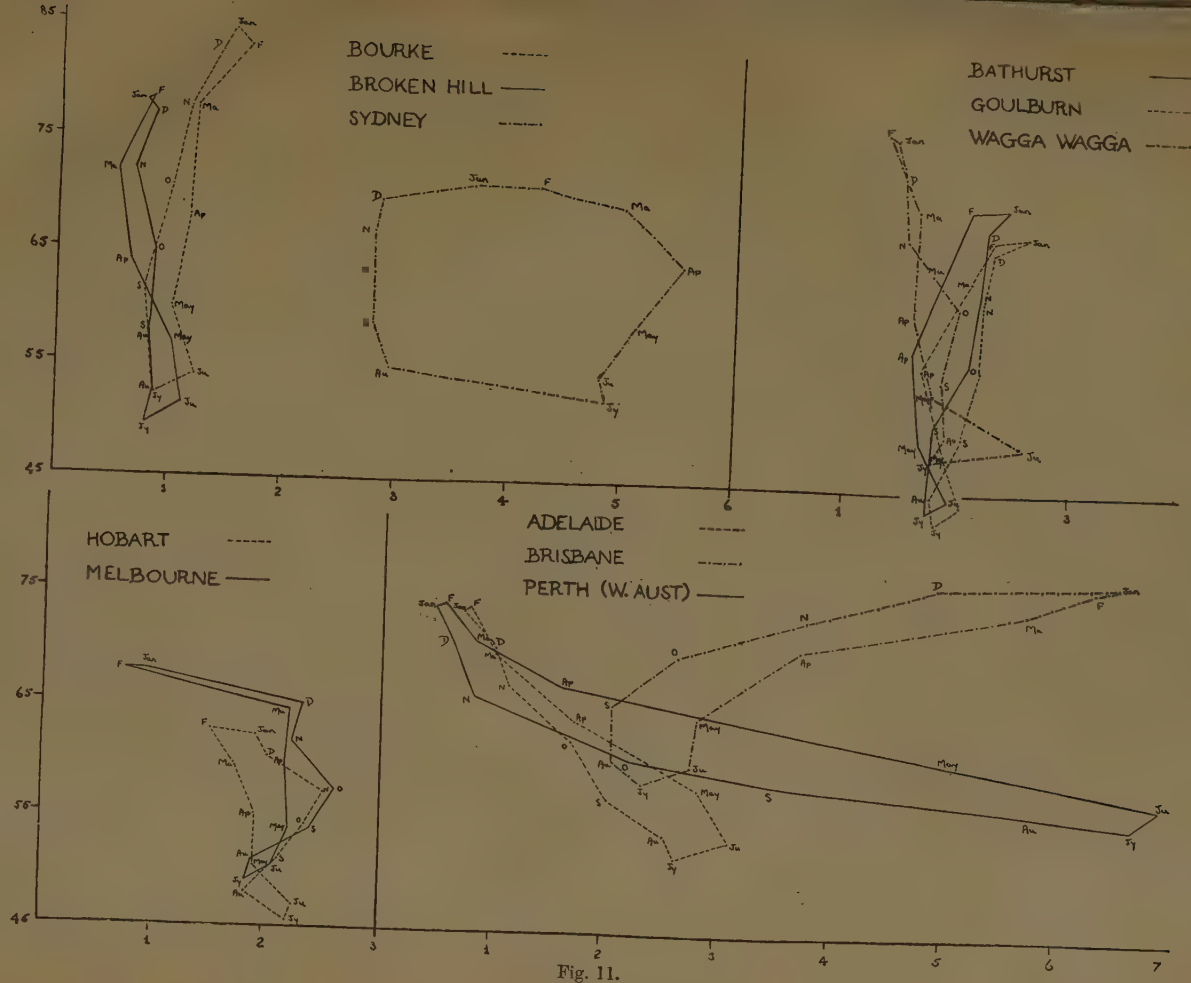

BOURKE
BROKEN HILL
SYDNEY
BATHURST
GOULBURN
WAGGA WAGGA
HOBART
MELBOURNE
ADELAIDE
BRISBANE
PERTH (W. AUST)

Fig. 11.

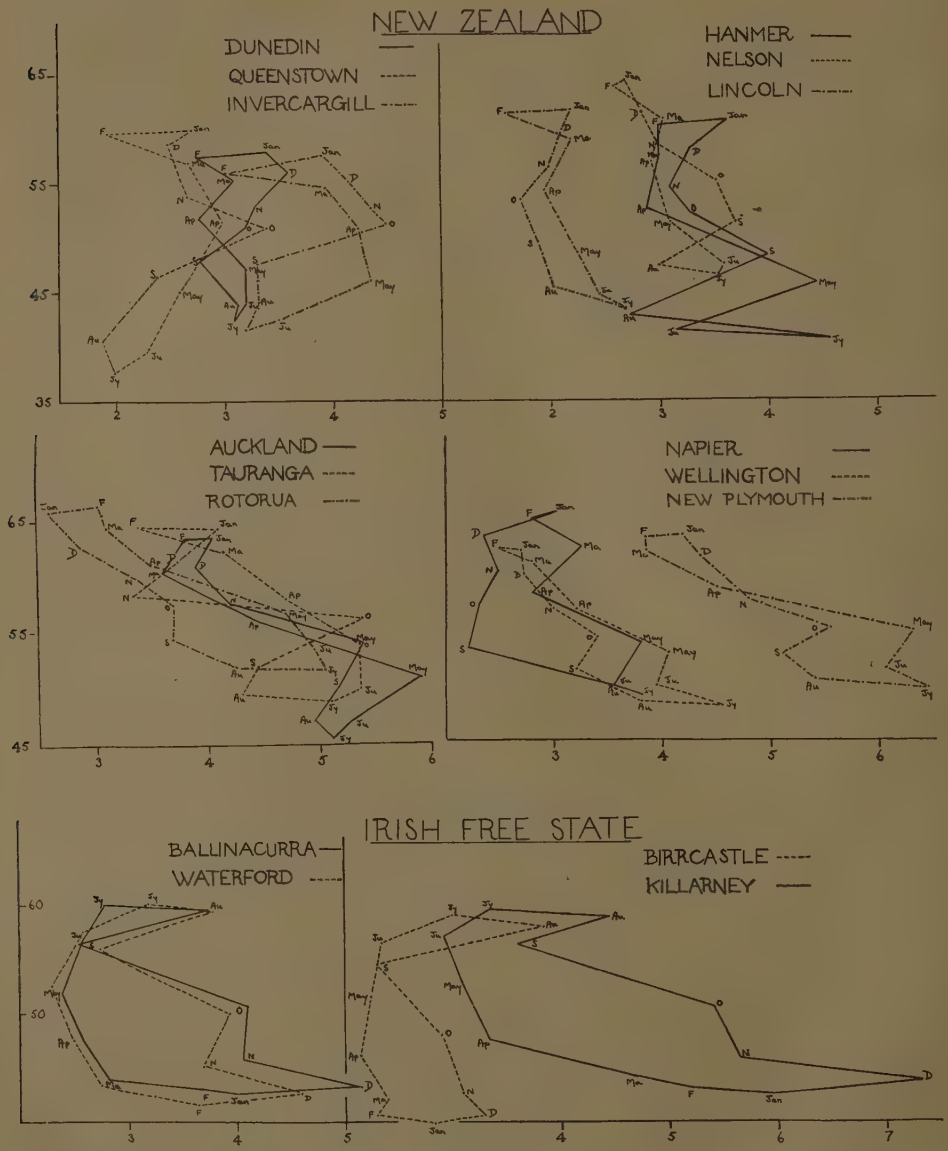

NEW ZEALAND
DUNEDIN
QUEENSTOWN
INVERCARGILL
HANMER
NELSON
LINCOLN
AUCKLAND
TAURANGA
ROTORUA
NAPIER
WELLINGTON
NEW PLYMOUTH
IRISH FREE STATE
BALLINACURRA
WATERFORD
BIRRCASTLE
KILLARNEY

Fig. 12.

Another factor which is to be considered is that of breed characteristics, particularly in respect of specialisation for ram or ewe breeding and of relation to other breeds for crossing purposes. For example, the Wensleydale might find suitable habitats in many parts of the South Island so far as climate is concerned, but it has relatively limited functions as a breed in its native localities.

Some of the discrepancies between breed graphs and New Zealand station figures when studied in detail illustrate further the effects which husbandry can exert and also bear upon questions of the critical periods.

The hythergraph for Lincoln station extends beyond the figures for the Leicester and Lincoln breeds in respect of temperature in December, January and February and exceeds that of the Border Leicester in temperature during the summer months; but the rainfall of the New Zealand station at this time is similar to that of the early summer months for these breeds in Britain. The temperature differences are not, however, excessive and could not be considered serious. For the Romney breed at this station, February appears rather dry—but the rainfall in this month is equivalent to that in May for the breed in its native land. At Napier the overlapping of the hythergraph with the inclusive figure of the Romney breed is reduced chiefly by temperature differences, the rainfall comes within the British range, and for the Border Leicester at this station the rainfall during the hot summer months is the same as that in early summer in Great Britain.

In general these expected distributions of the breeds exist to a great extent; the South Island is more remarkable for its numbers of the different British breeds than is the North Island, and Canterbury is one of the most successful centres of stud breeding for Down types as well as Longwools. This is particularly the case with regard to those breeds in which the New Zealand type is closely similar to the British; the Romney in this respect is an exception, the New Zealand Romney being of different type in conformation and constitution to the original Romney Marsh. The situation at Napier when the Leicester and Lincoln breeds are considered may be of interest. The Hawke's Bay district was formerly populated with large numbers of sheep of these breeds, but these are now replaced by the New Zealand Romney. Mortality as hoggets and shearlings contributed to the change. On comparing the temperature-rainfall graphs it is seen that the Napier hythergraph deviates from the breed figures by reason of excessive rainfall from May to August and in January and March (the latter month only in the case of the Leicester); and these differences coincide with the time at which the young animals would be 4–12 months of age.

Hythergraphs for four stations in the Irish Free State are also shown; applying this method of estimating climatic suitabilities, and numbering the various breeds in descending order of fitness, the following represents the expectations:

Breed	Ballinacurra	Waterford	Killarney	Birr Castle
Southdown	.	7	.	3
Suffolk	.	5	.	3
Shropshire	.	7	.	3
Hampshire	3	2	.	3
Oxford	2	2	.	3
Ryeland	1	1	(1)	2
Leicester	.	.	.	9
Lincoln	5	9	.	9
Romney	5	5	.	3
Border Leicester	3	2	.	1
Cheviot	.	.	.	3
Blackface	3	3	1	.
Welsh	1	1	2	2
Kerry Hill	2	2	2	1

It may be suggested tentatively that there is some evidence that these criteria might be usefully considered when it is necessary to assess the possibility of British breeds becoming established in districts away from their native localities. They must remain, however, as indefinite factors until their associations with other influences are more fully explored and their direct or indirect effects are determined.

IV. Summary.

1. The flock distribution of the numerous pure breeds of sheep in the British Isles is used as a basis for examining the distinctive conditions of altitude, monthly temperature and rainfall under which the several types exist.

2. The different plasticities of the breeds in relation to these environmental factors are discussed.

3. The average conditions of temperature and rainfall for any particular breed in its original localities being defined, a method is suggested whereby it may be estimated whether the situations in respect of these factors in other areas would be favourable to that type.

V. Acknowledgments.

The author is indebted to the Council of the Wool Industries Research Association for permission to publish this study and to the Empire Marketing Board, under whose grant part of the work was conducted. He wishes also to record his appreciation of the many helpful suggestions made by Prof. R. G. White of the University College of North Wales, throughout the investigations, and by Mr A. V. Williamson of the Department of Geography, the University of Leeds, in the presentation and discussion of the results.

REFERENCES.

(1) **Barkley, H. (1927).** "Forecasting a wool clip." Pastoral Review, 37, 759–61.

(2) **Bartholomew, J.** and **Lyde, L. W. (1928).** "An atlas of economic geography." Oxford Univ. Press.

(3) **Brown, W. (1870).** "British sheep farming." A. and C. Black, Edinburgh.

(4) **Cathcart, Earl (1875).** "Wool in relation to science with practice." J.R.A.S.E. 11, 309–47.

(5) **Hammond, J. (1932).** "Growth and development of mutton qualities in the sheep." Oliver and Boyd.

(6) **Heape, W. (1899).** "Note on the fertility of different breeds of sheep, etc." Proc. Roy. Soc. 65, 99–111.

(7) **Huntington, E. (1925).** "The distribution of domestic animals." Econ. Geog. 1, 143–72.

(8) **Johnson, E. L. (1924).** "Relation of sheep to climate." J. Agric. Res. 29, 491–500.

(9) **Low, D. (1845).** "On the domesticated animals of the British Islands." Longman, Brown, Green and Longmans, London.

(10) **Marshall, F. H. A. (1908).** "The effect of environment and nutrition upon fertility." Sci. Progr. 7, 1–9.

(11) **Nichols, J. E. (1927).** "Meteorological factors affecting fertility in the sheep." Zeit. Indukt. Abst. 43, 313–29.

(12) **Nichols, J. E. (1928).** "Estimates of the fleece weights of British sheep in relation to changes in distribution of types." Wool Record, 33, 1349–51 and 1413–17.

(13) **Nichols, J. E. (1928).** "The flock distribution of pure-bred sheep in Gt Britain." Wool Record, 33, 1559–63.

(14) **Nichols, J. E. (1928).** "Some aspects of the ecology of British sheep." J. Text. Inst. 19, T 329–33.

(15) **Taylor, T. G. (1919).** "The settlement of tropical Australia." Geog. Review, 8, 84–115.

(16) **White, R. G.** and **Roberts, J. A. F. (1927).** "Fertility and sex ratio in Welsh mountain sheep." Welsh J. Agric. 3, 70–9.

THE ROOK POPULATION OF THE UPPER THAMES REGION

By W. B. ALEXANDER, M.A., M.B.O.U.
(Director of the Oxford Bird Census, University Museum, Oxford.)

(With one Map and three Figures in the Text.)

I. Introductory.

In the spring of 1928 the Oxford Bird Census made counts of the nests in the rookeries of an area of 224 sq. miles round Oxford. In their report on this work Messrs E. M. and B. D. Nicholson (**15**) stated their conviction "that an intensive study of the rook carried out over a period of years with a high degree of accuracy is feasible and would yield results of far-reaching importance to economic ornithology." In 1930 a private donor gave a substantial sum of money for the continuance of the work of the Oxford Bird Census, on condition that sufficient funds were secured to cover the cost of operations for three years. This condition was fulfilled when the Empire Marketing Board and the Ministry of Agriculture gave grants for that period on the understanding that study of rooks would be continued.

In April, 1931, a second census of rookeries was undertaken, covering an area of 910 sq. miles, which had been surveyed during the previous winter to locate the rookeries. The area, which measures 35 miles from east to west and 26 miles from north to south, is shown on the accompanying map. It covers the greater part of the region drained by the Upper Thames and its tributaries. In altitude it ranges from about 140 ft. above sea-level near Moulsford on the Thames to 755 ft. at Britwell Hill in the Chilterns, to 815 ft. at Wyck Hill in the Cotswolds and to 856 ft. at Whitehorse Hill on the Berkshire Downs. The area above 400 ft. is shaded in the map.

Geologically the area is entirely within the belt of Jurassic and Cretaceous formations, ranging from the Lower Lias up to the Chalk. The outcrops run from south-west to north-east, the oldest beds being exposed in the north-west. Except on the hills, however, the formations are to a great extent covered by drift and alluvium.

II. The breeding population.

The map shows by a cross the position of each group of nests. Where, however, there are numerous groups in close proximity it is impossible to indicate each separately, and the positions of the crosses merely indicate the area covered by a scattered community. From a study of the map it will be

obvious that in many cases it is impossible to define a rookery. Accordingly the population has been treated on the basis of the squares on the 1-inch Ordnance Survey Map, which measure 2 × 2 miles, with an area of 4 sq. miles. The order of population in each square is shown in Fig. 1, which indicates an extremely irregular distribution. In Fig. 2 the squares have been grouped in

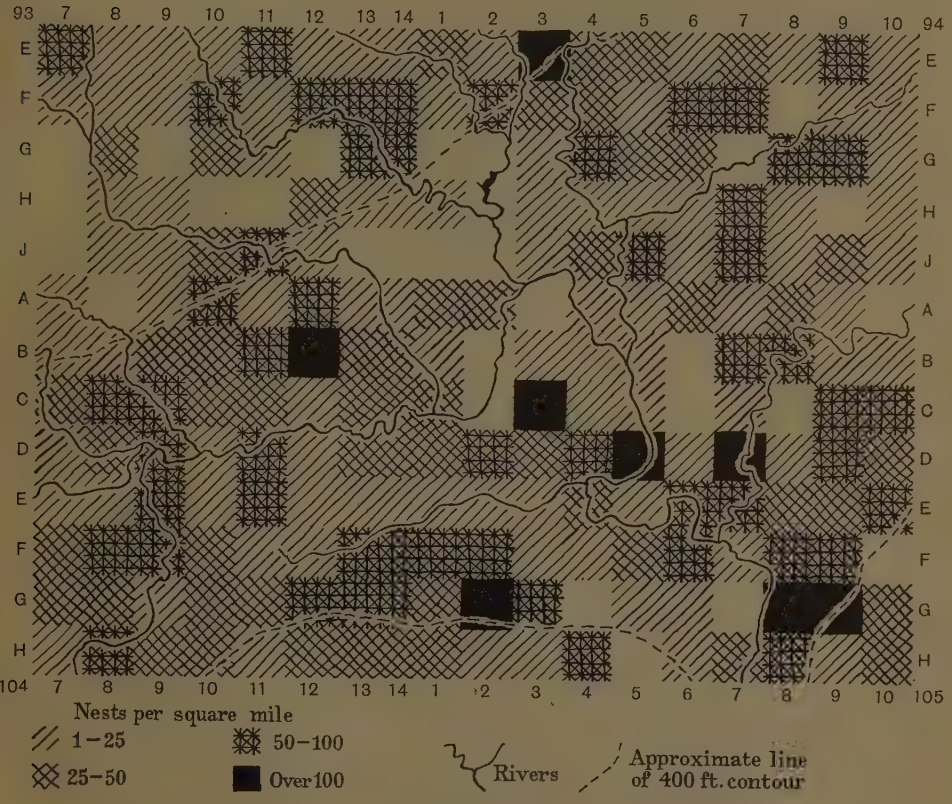


Fig. 1.

fours and the density in each of the resulting areas of 16 sq. miles is shown. In Fig. 3 the squares have again been grouped into twelve areas of either 64 sq. miles or rather more. The result of this grouping is naturally to smooth out minor irregularities, but considerable differences of density in different parts of the area are still apparent.

The map has been divided into six nearly equal regions and the numbers

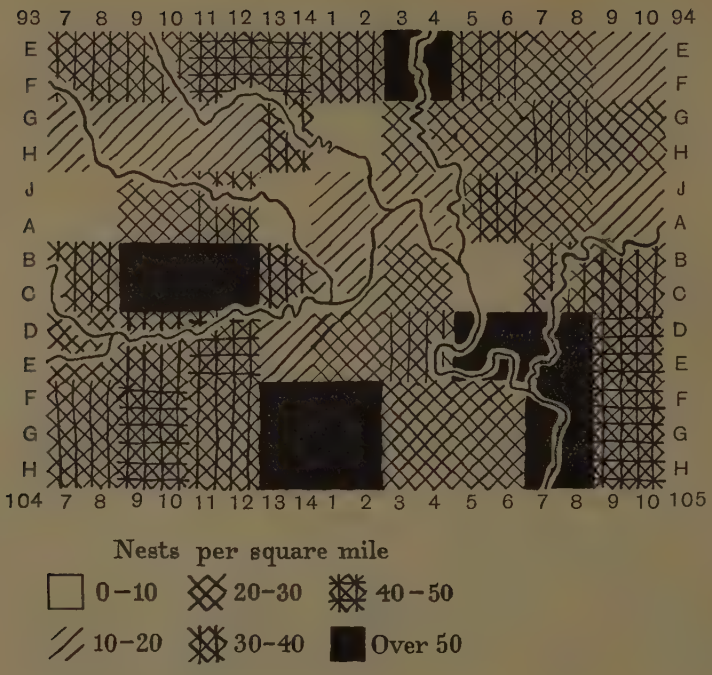

93 7 8 9 10 11 12 13 14 1 2 3 4 5 6 7 8 9 10 94
E F G H J A B C D E F G H
104 7 8 9 10 11 12 13 14 1 2 3 4 5 6 7 8 9 10 105
Nests per square mile
0–10
10–20
20–30
30–40
40–50
Over 50

Fig. 2.

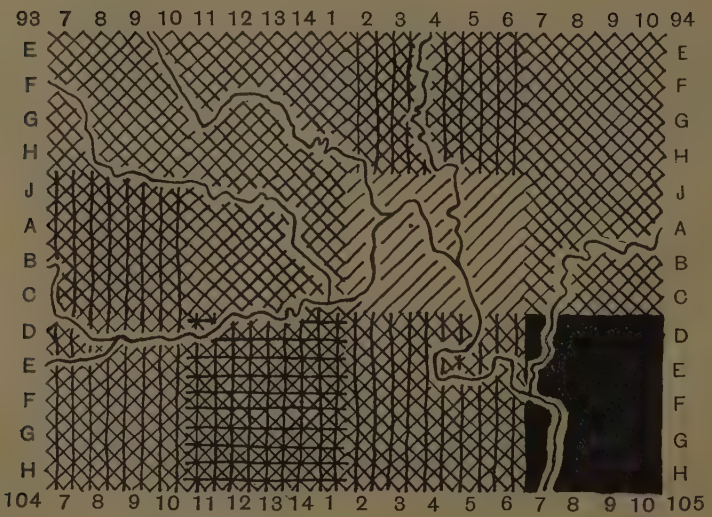

93 7 8 9 10 11 12 13 14 1 2 3 4 5 6 7 8 9 10 94
E F G H J A B C D E F G H
104 7 8 9 10 11 12 13 14 1 2 3 4 5 6 7 8 9 10 105

Fig. 3.

of nests in each and the total for the whole area are shown in the following table:

District	Area in sq. miles	Most central town included	No. of rook nests	Nests per sq. mile
N.W.	144	Burford	3,500	24
N.C.	132	Woodstock	3,550	26
N.E.	144	Bicester	3,800	26
S.W.	168	Faringdon	6,700	39
S.C.	154	Wantage	5,700	36
S.E.	168	Wallingford	7,250	43
Upper Thames	910	Oxford	30,500	33·5

III. FACTORS DETERMINING DISTRIBUTION.

The Nicholsons (**15**) suggested that three factors appeared to influence the distribution of rookeries in the area they surveyed: altitude, the proximity of rivers and the geological formation. Wynne (**21**), from his survey of the rookeries of the Isle of Wight, reached similar conclusions. It is of interest therefore to discover how far the data obtained for this much larger area support these findings.

Reference to the map will show that whilst rookeries occur above 400 ft. on the Cotswolds, Downs and Chilterns, the rooks seem to avoid those portions of the area of the Oxford Basin in which the land rises above that altitude. The only exceptions are at Blunsdon and Highworth in the south-west corner. On the three considerable areas of high ground crosses are obviously less numerous than in the Oxford Basin, but this might be due to the rookeries on the hills being more compact and not to a lower density. If all the squares shown in Fig. 1 are grouped according to altitude the result is:

Altitude of squares	Area in sq. miles	No. of nests	Nests per sq. mile
Entirely above 400 ft.	36	785	22
Traversed by 400-ft. contour	418	13,212	32
Entirely below 400 ft.	456	16,603	36

The difference in average density between the population of squares below 400 ft. and of squares partly below and partly above this altitude is hardly great enough to be significant. The few squares above 400 ft. have a decidedly lower density, but as eight out of the nine are on the Cotswolds this may be due to the geological formation of those hills and not to their altitude.

The table on p. 28 gives figures for the numbers in squares traversed by rivers, by streams named on the 1-inch maps and by no river or named stream. In cases where two rivers traverse the same square it has been assigned to the larger.

It will be seen that though the density is high in squares traversed by the Cherwell, Cole, Thame and Leach, it is low in those along the Ray, Windrush and Ock and approximates to the average along the Evenlode and Thames.

There is little doubt that in squares traversed by streams or rivers the rooks tend to build in the neighbourhood of the water, but the figures make

it evident that such squares are no more attractive to rooks than those without streams.

Squares traversed by	Area in sq. miles	No. of nests	Nests per sq. mile
Thames	136	4,834	36
Coln	12	195	16
Leach	24	978	41
Cole	24	1,109	46
Windrush	62	1,337	22
Dikler	12	417	35
Evenlode	58	1,855	32
Glyme	22	586	27
Dorn	4	13	3
Cherwell	40	1,869	47
Ray	32	535	17
Ock	32	764	24
Thame	40	1,732	43
Rivers	498	16,224	33
Named streams	216	7,761	35
No river or stream	196	6,515	33

The number of squares entirely situated on a single geological formation is only small. The figures available are shown in the following table:

Squares entirely on	Area in sq. miles	No. of nests	Nests per sq. mile
Chalk	28	1354	48
Corallian	4	263	66
Oxford Clay	24	541	23
Great Oolite	24	402	17
Lower Lias	4	392	98

The areas of Corallian and Lower Lias are evidently too small to be significant. The soils derived from the other three geological formations are described by Morison (**12**) as follows. Chalk: light variable loam, resistant to drought; good barley land, grass very poor. Oxford Clay: heavy clay; nearly all under poor grass. Great Oolite: variable stonebrash; excellent for sheep, grass very poor.

The above figures suggest that the loamy soil on the chalk is preferred by rooks to the heavy clay or the stonebrash.

Reference to Figs. 1, 2 and 3 will show that there is an area much below the average density rather to the north of the centre of the map. It extends from Woodstock and Witney south-east to include Oxford and its immediate neighbourhood. Here a block of twenty-three adjacent squares with an area of 92 sq. miles contains only 1085 nests, giving the very low density of twelve nests per sq. mile. Evidence has been obtained that in the town of Woodstock and the parks of Blenheim and Eynsham Hall, where there are now no rookeries, there were rookeries of considerable size within the memory of elderly people. It seems clear therefore that it would be unwise to explain the present scarcity of rooks in the area on grounds of geological formation or altitude. Part of this area was within the region surveyed in 1928 and the Nicholsons (**15**) suggested that the scarcity of rooks was due to the abundance of jackdaws, which find suitable nesting sites in the trees in Blenheim Park.

The evidence that jackdaws are more numerous in this region than in other parts of the district does not seem convincing.

It is not impossible that at some period the owners of some of the estates in the area may have adopted a deliberate policy of destroying rooks. The absence of rooks in several squares on the Cotswolds in the north-west corner of the map is reported to be due to their destruction on two large estates. On the other hand, the square with the highest total of nests, 753, is that which includes the town of Wallingford, and it is reported that one or more estate owners here refuse to allow the rooks to be shot.

IV. CHANGES IN THE AREA SURVEYED IN 1928.

Of the 101 rookeries listed by the Nicholsons (**15**) in the area of 224 sq. miles surveyed in 1928, seventeen had disappeared in 1931, all of them rookeries with less than fifteen nests, and five of them in the City of Oxford. On the other hand, rookeries were found in 1931 at fifteen sites not recorded in 1928, and evidence was obtained that two of these rookeries had been in existence for many years. One of these, at Kingston Bagpuize, had eighty-six nests; the other, at Draycott Farm, Longworth, had fifteen nests in 1931, but in 1928 it was leased for shooting on the basis of eighty-five nests, though this figure was disputed. The greater part of the rookery in Shotover Park was also overlooked in 1928 when only fifty-three nests were counted there, whilst in 1931 there were 266. It seems probable therefore that about 370 nests were overlooked in the 1928 census, and that the number in the area in that year was about 7100. In the same area in 1931 the number of nests counted was 7281, so that there was probably an increase in the three years of rather less than one nest per square mile.

Of the eighty-four rookeries listed in 1928 which were still in existence in 1931, thirty-six had increased in size and forty-seven had diminished. In general, small decreases in the majority were more than counterbalanced by large increases in a few rookeries. The Marcham Park rookery increased from 297 to 500, and the Besselsleigh rookery from 176 to 302. Of the new rookeries only one was in Oxford, at Upper Wolvercote on the edge of the city, and it is evident that Oxford is becoming too large for rooks to continue to nest in the centre of the city. Since 1931 two more Oxford rookeries have been deserted.

The Nicholsons (**15**) suggested that in large scattered rookeries the ends might lose touch and thus two rookeries be derived from a single one. No such process appeared to have taken place in any rookery since their survey, but, on the other hand, there were two cases in which rookeries which they considered distinct had since become united by the building of nests in the space between them.

In addition to the figures obtained in 1928 figures for a good many of the rookeries in the district have been kindly supplied by Mr Venables, the Oxford

gunsmith. Figures from the same source were published by Gunther (7), but he did not disclose their origin. In every case these figures show a decline with fluctuations, but in some of the rookeries there appears to have been a marked increase during the war. Gunther's conclusion that prior to the war rooks in the district were decreasing was based mainly on these figures. They are, however, the figures for those rookeries in the district at which the shooting rights were offered for lease. It is only natural to suppose that the lessees, who pay about £5 per 100 nests, would shoot there more frequently than would be the case in a rookery shot by the owner and his friends. The figures for Great Copse, Chiselhampton, which still remains the largest rookery in the district, are as follows: 1890 or earlier—1500; 1909—1000; 1911—660; 1914—300; 1925—650; 1928—683; 1931—619. The longest series of figures available is for Pinkhill Farm, Eynsham, where the number of nests is given as: 1909—150; 1911—165; 1912—135; 1913—138; 1914—150; 1922—325; 1923—170; 1925—200; 1927—180; 1928—122; 1929—205; 1930—100; 1931—85. During the last two winters many of the elms containing the nests were blown down.

V. Comparison with other areas.

Surveys of rookeries have been made in a good many areas at different times, in some cases by estimating the numbers of nests in each rookery, in other cases by actual counts. In very few cases has any statement been made as to the time of year when the counts or estimates were made. The following figures for rookeries in the Upper Thames district, where two counts were made in the spring of 1931, indicate the importance of deferring counts till as late as possible:

Swyncombe House	March	10	89 nests	April	4	133 nests
Stanford Park Farm	,,	11	99 ,,	,,	15	276 ,,
Buckland Park	,,	23	50 ,,	,,	15	57 ,,
Pinkhill Farm	,,	31	83 ,,	,,	30	85 ,,
Littlemore	April	2	14 ,,	,,	28	18 ,,
Radley Park	,,	2	67 ,,	,,	28	68 ,,

It is obvious that estimates or counts made earlier than April are likely to give a figure decidedly too low.

In the table on p. 31 all known data as to rook populations are collected, but some of the results are certainly not very reliable. The surveys are arranged in ascending order of density.

It will be seen that the only densities higher than that found round Wallingford are those for Edinburgh (only 51 sq. miles) and Berwickshire (based on very rough estimates). The Upper Thames district appears to have a higher density than any other considerable area whose population has been counted accurately. This is no doubt partly due to the fact that little of it is unsuited to rooks, whilst most other regions that have been surveyed contain considerable areas of moorland, hill pasture or woodland, types of country

District	Date of survey	Area in sq. miles	Approx. no. of nests	Nests per sq. mile	Reference
Holland	1924	12,760	31,000±	2·5±	Anon. (3)
Harrow	1928	50	84	2	Harrisson (8)
,,	1929	50	55	1	,,
,,	1930	78	361	5	,,
,,	1931	78	278	4	,,
North Wales	1920–7	*c.* 1,750	*c.* 8,000	5	Walton (20)
Aberystwyth	1913–16	*c.* 250	*c.* 1,550	6	,,
Nottinghamshire	1928	963	6,500	7	Roebuck (16)
Leicestershire	1928	819	9,400	11	,,
East Midlands	1928–30	5,300	64,000	12	,,
Dumfriesshire	1908	1,106	17,500+	16+	Gladstone (5)
,,	1921	1,106	16,000+	14+	Gladstone (6)
Midlothian	1928	366	5,820+	16+	Nash (14)
Wirral Peninsula	1928–9	90	1,700	19	Marples (10)
Lanarkshire	1922	880	18,800	21	Stewart (17)
,,	1929	880	23,800	27	Stewart (19)
Isle of Wight	1932	146	4,200	29	Wynne (21)
Oxford	1928	224	6,750	30	Nicholson (15)
Edinburgh	1921	51	1,545	31	Evans (4)
,,	1928	51	2,280	46	Nash (14)
Berwickshire	1887	464	21,000±	45±	Muirhead (13)

generally avoided by rooks. For those regions for which figures are available the numbers of acres of agricultural land (arable and permanent grass) per rook's nest have been calculated. In cases where parts of counties only have been surveyed it has been assumed that they are typical of the counties as a whole. The results are as follows:

Upper Thames district, Isle of Wight, Dumfriesshire (1908)—1 rook's nest to 15 acres of agricultural land; Wirral Peninsula—1 nest to 18 acres; East Midland counties (Derby, Notts, Leicester, Rutland and Lincs)—1 nest to 46 acres; Aberystwyth district—1 nest to 56 acres; North Wales (Anglesey, Carnarvon, Denbigh and Flint)—1 nest to 84 acres.

VI. The winter population.

Available figures indicate that on the average each pair of breeding rooks produces four eggs, and that from these they rear two young. Of these, on the average, one per nest is shot, leaving one to accompany the old birds when they leave the rookery and lead a more or less nomadic existence during the late summer. During this period there is undoubtedly a considerable further mortality among the young birds, so that when the rooks settle down to their winter habits there is probably about one young bird surviving to every four adults. In a stationary population it is clear that of these five birds one must succumb during the winter.

The most striking feature of the winter habits of rooks is their assembly in great numbers at dusk to roost. The roosts are generally, but not always, close to, or in the same trees as, a large rookery. There is good reason for thinking that in most cases where a roost is not at a rookery there was formerly a rookery at the site but that for some reason the rooks have ceased to breed there.

For instance, Gladstone (**5**) gives particulars of three roosts in Dumfriesshire where the rooks had ceased to nest 33, 20 and 9 years previously respectively. Borrer (**2**) in 1891 mentions a roost in Sussex at a place where prior to 1876 there was one of the largest rookeries in the county. Evans (**4**) in 1922 records that rooks still roosted at Crow Wood, Penicuik, until the war the largest rookery in Midlothian. There can be no doubt that the same roost has in many cases been used by the rooks of a district for a great many years, and we have only found two records of roosts being started in new places: Babington (**1**) records that about 1880 birds began to roost at a rookery in Suffolk which they had previously only frequented in the breeding season, and Gunther (**7**) mentions that in 1911 rooks formed a roost in Middleton Park, Oxon, but were driven away in subsequent seasons. There was then, and still is, a considerable rookery in this park.

The positions in the winter 1931–2 of the roosts in the area of 910 sq. miles whose rookeries were counted in 1931 are shown by circles on the map. These are ten in number and there are four others a short distance outside the area to at least three of which birds travel from within the area. The following is a list of them with particulars of the size of the rookery at which twelve out of the fourteen are situated:

Roost	No. of nests in rookery (1931)
A. Sherborne Common, Glos	— (191 a mile away)
B. Bruern Abbey, Oxon	392
C. Ranger's March Wood, Shorthampton, Oxon	346
D. Kirtlington Park, Oxon	387
E. Old Paddock Wood, Rycote Park, Oxon	85
F. Great Copse, Chiselhampton, Oxon	794
G. Marcham Park, Berks	500
H. Grove Wood, Faringdon Park, Berks	476
J. North Leaze Wood, Hannington, Wilts	— (209 a mile away)
K. Bradwell Grove, Oxon	76
L. Shelswell Plantation, Oxon	Large
M. Chearsley Furze, Bucks	,,
N. Whatcombe Wood, South Fawley, Berks	,,
P. Oaken Grove, Fawley Court, Bucks	*c.* 550

Mellersh (**11**) in 1902 mentions a roost in Sherborne Park, but the present roost is nearly a mile outside. C was recorded by Gunther (**7**) in 1917, and a resident in the neighbouring village said that rooks had roosted there as long as his grandfather could remember. Local residents also testified that H, J and K had been there as long as they could remember, 30, 40 and 33 years respectively.

During the daytime the birds from each roost, in flocks of varying size, disperse over the surrounding country to feed, and we have obtained considerable evidence that flocks from different roosts may feed together and separate towards evening to fly to roosts in opposite directions. Birds belonging to one roost may even range into the neighbourhood of another. In other words, the communities appear to have no definite feeding territories

As the breeding season approaches the birds gradually spend more and more time at their rookeries and, especially in February, they usually remain at them till dusk and then fly straight to the roost. It thus becomes possible to determine which rookeries contribute to each roost and thus to outline the breeding territory of each roost-community or tribe of rooks.

The broken lines surrounding each roost on the map show the breeding territory of the tribe as far as it had been ascertained in 1932, but, especially in the western part of the map, there are still numerous rookeries whose tribal affiliations are not yet known. The arrows indicate the directions of the three roosts outside the map whose territories extend within it.

A study of the map shows that the roosts are by no means promiscuously placed. Firstly, they are all below the 400-ft. contour, though roost N, which is not on the map, is at an altitude of about 500 ft. on the Downs. Secondly, roosts J, H, G, F, E and M are approximately equidistant from one another and from the escarpment of the chalk hills (Downs and Chilterns). It seems probable that the escarpment is actually the boundary of the territories of these roosts and that there is another series of roosts on the southern slopes of the hills, of which N and P are two, whose territories extend north to the ridgeway. Thirdly, it seems worthy of note that Oxford appears to be the meeting-point of the territories of roosts D, E, F and G. Evans (**4**) records that rooks from opposite sides of Edinburgh go to different roosts and Stewart (**18**) finds the same at Glasgow. Stewart's study of the rooks in Lanarkshire is the only similar work of which we are aware. Though Lanarkshire is one of the most natural counties in Britain, coinciding almost exactly with the basin of the Clyde, only two of the tribes have territories confined to the county, four other roosts in adjacent counties having territories extending into Lanarkshire. It is clear therefore that ridges of hills are not always boundaries between adjacent territories. Stewart found that the different tribes had different feeding habits and that the great increase in the number of nests between 1922 and 1929 was almost entirely in the territory of one tribe. As however this was a tribe whose roost was outside the county it does not seem certain that the tribe had actually increased. It may be that for some reason a larger proportion of the tribe had taken to breeding in the Lanarkshire portion of its territory. In this connection it is worth mentioning that the two rookeries in the Oxford district noted above as having shown the greatest increases between 1928 and 1931 are both in the territory of roost D.

Attempts have been made to count the birds coming to roost at several of the roosts in the Upper Thames district by posting observers in a circle round them during the afternoon. The results are not very satisfactory, chiefly because the majority of the birds come in in large flocks when it is almost dark, and because of the difficulty of discriminating rooks from jackdaws. The results are shown in the following table, which also shows the expected

population of each roost based on the number breeding within its territory in 1931. As we have seen, the young birds may be expected to increase this population by perhaps 25 per cent. at the beginning of winter:

Roost	Date of count	Approximate numbers of Jackdaws	Approximate numbers of Rooks	Expected population of rooks	Comments
F	19. xi. 30	2,000	4,500	7,900	Also three carrion crows. The position of this roost makes it difficult to find satisfactory viewpoints
F	3. xii. 30	5,500+		7,900	Very bad visibility. Count incomplete
G	18. xi. 31	2,800+	6,600+	9,200	Very poor visibility. Count incomplete
G	17. xi. 32	6,500	12,500	*c* 15,000	Also one magpie
E	25. xi. 31	6,500	5,500	*c.* 5,000	— —
E	24. xi. 32	6,000	4,000	*c.* 7,000	Birds not all in before dark
C	24. i. 32	9,000	12,000	*c.* 11,000	Also two carrion crows

It will be seen that there is some approach to agreement between the expected populations and the numbers counted. In the case of roosts E and C the territories extend outside the area in which the nests have been counted, so the expected population can only be given roughly. It is noteworthy that both counts at E gave more jackdaws than rooks[1].

The main object of the counts was to ascertain whether the rook population was larger in winter than in the breeding season, and there is enough agreement between the two sets of figures to show that the population is of the same order at both seasons. It is known that large numbers of rooks arrive on the east coast of England in autumn from the Continent and depart again in spring. But it seems clear that no considerable number, if any, penetrate to the Upper Thames district. Harrisson (**9**) gives particulars of the large roost at Madingley, near Cambridge. It was estimated to contain 10,000 rooks and the minimum breeding population within its territory is said to be 7000 birds, so that even in Cambridgeshire few foreign rooks would appear to be present in winter. Similar studies in East Anglia, Lincolnshire and Yorkshire would be of considerable interest and importance. The only ringed rook from abroad yet recovered in the British Isles was obtained in the East Riding of Yorkshire in December, 1930, and had been ringed on October 31st, 1927, at a lightship off the island of Borkum in the North Sea.

VII. Acknowledgments.

We are indebted to many landowners and estate agents for permission to count nests on their properties, also to the following for assistance in making the survey and the census of nests: J. K. Adams (Oxford), J. A. G. Barnes (Queen's), R. J. O. Bray (Balliol), Mrs Bretherton (Boar's Hill), J. H. S. Buchan (Elsfield), W. A. Cadman (Keble), Miss D. M. Campbell (Oxford),

[1] In the winter 1932–3 rooks ceased to roost at F, those from Chiselhampton itself going to roost at E, whilst those from the rest of the territory apparently went to G.

COTSWOLDS
HEYFORD HILL
R. RAY
R. GLYME
WOODSTOCK
BLENHEIM LAKE
R. CHERWELL
WYCHWOOD FOREST
R. EVENLODE
BURFORD
R. WINDRUSH
WYTHAM HILL
CUMNOR HURST
BOARS HILL
R. LEACH
R. THAMES
R. COLN
FARINGDON
R. OCK
R. COLE
COLES HILL
COXWELL HILL
HIGHWORTH HILL
BLUNSDON HILL
FRIARS HILL
STANTON HILL
VALE OF WHITE HORSE
WANTAGE
SWINDON
LAMBOURN DOWNS
A
B
C
D
G
H
J
K

W. D. Campbell (Charlbury), P. Crosfield (Witney), W. Dockar-Drysdale (Radley), Mrs Evetts (Tackley), Miss J. Orr Ewing (Oxford), J. K. Henderson (Studley), Sir A. Hirtzel (Fairford), A. Hodgkin (Oxford), I. G. Philip (Queen's), R. B. Pugh (Queen's), Mrs Radford (Oxford), M. G. Robinson (St Edmund Hall), A. F. Smith (Swindon), A. G. Tayler (Bourton-on-the-Water), Mrs Thomas (Oxford), Dr A. Waterhouse (Oxford), C. E. Wigg (Hinksey), J. D. Wood (Queen's), and H. G. Woodall (Keble).

In making the counts at roosts assistance was received from many members of the Oxford Ornithological Society and at the Shorthampton roost from Mr W. D. Campbell and some of his pupils at Charlbury school.

REFERENCES.

(1) **Babington, C. (1884–6).** "Catalogue of the birds of Suffolk."
(2) **Borrer, W. (1891).** "The birds of Sussex."
(3) **Anon. (1925).** "De Roek in Nederland." Verslagen en Mededeelingen van den Plantenziektenkundigen Dienst te Wageningen, No. 39.
(4) **Evans, W. (1922).** "Edinburgh rookeries in 1921." Scott. Nat. pp. 9–12.
(5) **Gladstone, H. S. (1910).** "The birds of Dumfriesshire."
(6) **Gladstone, H. S. (1923).** "Notes on the birds of Dumfriesshire."
(7) **Gunther, R. T. (1917).** "Report on agricultural damage by vermin and birds in the counties of Norfolk and Oxfordshire in 1916."
(8) **Harrisson, T. H. (1931).** "Birds of the Harrow district." London Nat. pp. 82–120.
(9) **Harrisson, T. H. (1932).** "The study of a rook roost." Rept. Cambridge Bird Club for 1931, pp. 22–9.
(10) **Marples, B. J. (1932).** "The rookeries of the Wirral Peninsula." J. Anim. Ecol. 1, 3–11.
(11) **Mellersh, W. L. (1902).** "A treatise on the birds of Gloucestershire."
(12) **Morison, C. G. T. (1916).** Chapter on Soils in Orr's "Agriculture in Oxfordshire," pp. 171–94.
(13) **Muirhead, G. (1889).** "The birds of Berwickshire."
(14) **Nash, J. K. (1928).** "The rookeries of greater Edinburgh and Midlothian." Scott. Nat. pp. 69–75.
(15) **Nicholson, E. M. and B. D. (1930).** "The rookeries of the Oxford district." J. Ecol. 18, 51–66.
(16) **Roebuck, D. (1932).** Rept. Brit. Assn. Adv. Sci., York, p. 332, and The Times, Sept. 3.
(17) **Stewart, W. (1923).** "The rook in Lanarkshire." Scott. Nat. pp. 141–6.
(18) **Stewart, W. (1924).** "Roosting habits of Lanarkshire rooks." Scott. Nat. p. 69.
(19) **Stewart, W. (1930).** "The rook in Lanarkshire, 1922–29." Scott. Nat. pp. 15–21.
(20) **Walton, C. L. (1928).** "Rooks and agriculture in Mid and North Wales." Welsh J. Agric. 4, 353–6.
(21) **Wynne, J. F. (1932).** "The rookeries of the Isle of Wight." J. Anim. Ecol. 1, 168–74.

CONTRIBUTIONS TOWARDS A SURVEY OF THE PLANTS AND ANIMALS OF SOUTH HAVEN PENINSULA, STUDLAND HEATH, DORSET

III. ORTHOPTERA[1]

By C. DIVER and P. DIVER.

(With Plates I–III and four Figures in the Text.)

CONTENTS.

		PAGE
I.	The scope of the enquiry	36
II.	Description of the area	37
III.	The vegetation of the locus types	39
IV.	The species found	43
V.	Methods	44
VI.	The general grasshopper population	44
VII.	Problems of distribution	46
VIII.	Recent physiographical changes	47
IX.	The distribution of the species in relation to habitat type and "geographical" spread	47
	(*a*) Absentees	49
	(*b*) Species of limited distribution	49
	(*c*) Species of wider distribution	53
X.	Factors limiting the range of loci occupied by different species	63
XI.	The grasshopper communities	65
XII.	Population intensity	67
XIII.	Summary	69
	References	69

I. The scope of the enquiry.

The enquiry was planned to determine, first, the number of species inhabiting a defined area and their distributional relationships both to each other and to the various plant communities, and, secondly, the variation within limited populations. A suitable time for such an enquiry is the early autumn, for the majority of species are by then normally adult. The work was actually carried out during the last fortnight of August, 1931. The weather conditions of that year made it impossible to carry out the full programme; however, the data collected appear to be of sufficient interest to warrant their publication.

Generally speaking the poor summer resulted in a "late" year. How far this effected a delay in the life cycle of the Orthoptera we are unable to say,

[1] I, Physiography (C. Diver), in press, and II, Flowering plants and ferns (R. D'O. Good), in preparation.

as we have made no control collections in an "early" or a normal year. In most of the species a fair proportion of nymphs were still found. This was particularly noticeable in the two Tetrigid species, where the nymphs far outnumbered the adults.

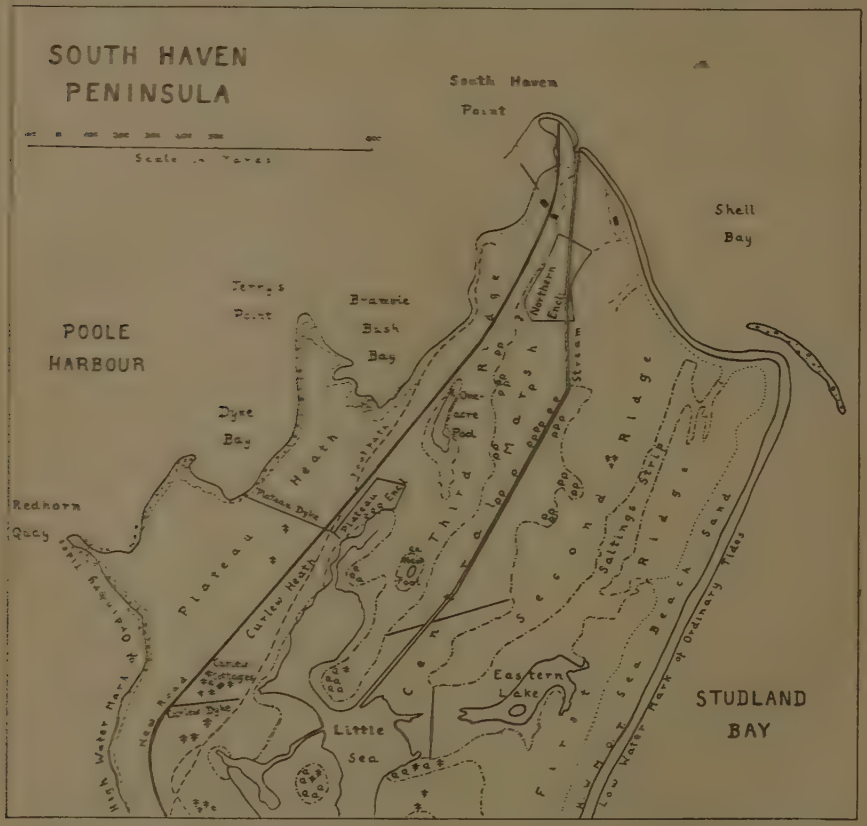
Unfortunately, the conditions were not really suitable for obtaining population samples on any of the collecting days. On most days there was a high wind and on none was there continuous sunshine. Consequently the visible population, particularly of the Acridid species, was smaller than we had been led to expect. It became obvious that we could not obtain population samples of a sufficient size for statistical treatment, and the work was of necessity confined mainly to mapping the distribution of the species.

II. Description of the area.

The area chosen, which for lack of a better name we have called South Haven Peninsula, was the strip of low-lying, uninhabited land that runs northwards from Studland Heath to South Haven Point, enclosing on its westward side the southern part of Poole Harbour (Text-fig. 1). For reasons of expediency the grasshopper survey was limited to so much of South Haven Peninsula as falls within "Dorset Sheet LI 9" of the 25 in. Ordnance Survey (see Text-figs. 3 and 4). (The surveys undertaken since 1931 cover the whole of the peninsula, including some 250 acres to the south of the area considered here.) Within these limits, roughly a mile square, there are about 500 acres of land and fresh water. Until about six years ago there was no road, but now a main road connects South Haven Point with Studland and the Isle of Purbeck. Beyond providing, in its grassy sides, an improved habitat for some of the Acridid species, this has, as yet, hardly interfered with natural conditions at all. The remains of a cottage used to exist near South Haven Point, but now there are several wooden huts and the road has been embanked. The Point was excluded from this survey as it is mainly a sandy spit, and though interesting botanically provides little scope for a population of grasshoppers. Towards Studland Heath there are the ruins of a small building known as Curlew Cottages. No one has actually lived on this land now for a number of years. Interference with natural conditions is negligible. The road is used mainly for through traffic; and those visitors who do not pass through, mostly confine their attentions to the seashore. While these conditions obtain, the area is one admirably suited to ecological work.

On the seaward side, facing approximately east-south-east, there is a broad, sandy beach backed by low dunes not more than some 15 ft. at their highest and partially fixed by dune grasses. They occupy about 42 acres of our area, as the north-east shoulder was not surveyed (compare Text-fig. 1 with Text-fig. 3). The broad crest of this "First Ridge" slopes away on the landward side to a flat belt of saltings ("Saltings Strip") which runs from the north-east shore until it merges imperceptibly into "Eastern Lake." (As

only some of the physical features have official names it has been necessary, as an aid to concise description, to invent names for the others.) Behind these "slacks" and running parallel to them is a line of older heather-covered dunes ("Second Ridge"), which rapidly rise to their maximum height of between 20 and 30 ft. and gradually fall away southward until they run out



Text-fig. 1. Map of the northern part of "South Haven Peninsula" based upon the Ordnance Survey Map as revised to 1924, with the sanction of the Controller of H.M. Stationery Office. The road and "New Pool" have been sketched in.

into the lakes or the central marsh. From the lakes in the south runs a sluggish man-made drainage stream, flanked on either side by "Central Marsh." Towards the north this marsh dies away and the stream, passing into the *Juncus* beds of "Northern Enclosure," runs out through saltings near South Haven Point. The area west of the stream is more varied. Between Central Marsh and the road low heather-covered knolls, outliers of the third dune

ridge ("Third Ridge"), rise here and there above the general level. A few small clumps of sallow and birch (*Salix* and *Betula*) are to be found, and there is a small isolated pool ("One-acre Pool"). In the south the land rises westwards from Little Sea to form a low heather-covered plateau ("Curlew Heath" east of road, "Plateau Heath" west of road), which slopes away northward until submerged by Third Ridge. By the northern arm of Little Sea there is an oblong grassy enclosure ("Plateau Enclosure").

There are thus several distinct types of locus:

(1) Marram (*Psamma*) dunes.
(2) Saltings.
(3) The lakes.
(4) Swamp.
(5) Marshy spots and damp hollows.
(6) The low, open heather growing on the borders of other types (e.g. (1) and (2)).
(7) The second and third heather-covered sandy ridges.
(8) The heather-covered plateau.
(9) The enclosed grassy area of the plateau.
(10) The roadside.
(11) The harbour shore.

The geology of the area is simple. Bagshot beds are exposed over the whole of the heather-covered plateau, that is west of Little Sea and of a line joining its northern tip with the middle of Bramble Bush Bay. In the rest of the area the beds are covered by blown sand, except Northern Enclosure and over a few acres to the north and south of it which are marked as alluvium.

III. The vegetation of the locus types.

(1) *Marram dunes.* The seaward face of the dunes rises from the open sand of the beach and carries tufts of dune grasses but no other plants. This is equally true of the crest except that in a few of the dips occasional low plants have established themselves. These increase in number on the landward slope and clumps of heather and lichens and mosses begin to appear as the dunes merge into type (6).

(2) *Saltings.* The predominant plant of the saltings is the rush, *Juncus maritimus*. In the drier parts of Saltings Strip there is little else save grasses with low plants in the open patches. With increasing wetness bog myrtle (*Myrica Gale*) appears, chiefly on the borders, and other marsh plants increase in number, until these in turn give way to more truly aquatic plants.

(3) *The lakes.* Where a defined margin exists to Eastern Lake (i.e. round its two eastern arms) there is a border of bog myrtle and rushes. Apart from this, the margin as marked in 1924 could not be traced in 1931, when there was at least a foot of water in the middle of the saltings 150 yards north of

the surveyed margin. Similar encroachments were observed to the south and east. Since the water is nowhere more than 1 ft. 6 in. deep, *Juncus* and *Scirpus* grow right out into the lake (Pl. III, phot. 5). Round the western end, up to and beyond the dyke, there is dense swamp of type (4) (Pl. I, phot. 2). Little Sea and its arms are somewhat different. Most of the margin is surrounded by dense swamp from the lake edge of which tall sedges (*Scirpus*) and in some places rushes and reeds (*Phragmites*) grow a little way into the lake, but the greater part of the area is open water with no aerial vegetation. The general depth of this water is not known to us, but it is certainly several feet deeper than Eastern Lake. The south-west shore of Little Sea, the western extension and its connecting channel were not examined (except for the western end of the extension due south of Curlew Cottages), owing to the thick barrier of gorse (*Ulex*), birch scrub and bracken (*Pteris*). One-acre Pool to the north is again of a different type. On its eastern side there is a moderately well-defined margin with a narrow border of low plants, grass, bog myrtle, *Sphagnum*, sundew (*Drosera*) and rushes. At both ends the pool tails off into marsh with tussocks of grass (*Molinia caerulea*), rushes and some bog myrtle. The western margin is different. In the northern part the roadside is close, and a grass community with some patches of open sand runs near to the pool; but along the greater part of this side there is no defined margin, and the water runs out through tussocks of *Molinia* and bog myrtle with here and there *Sphagnum* and open patches of low bog plants. Most of the water surface of the pool is covered by aquatic plants (e.g. *Hypericum elodes* and *Menyanthes*).

(4) *Swamp.* The most pronounced swamp is to be seen on either side of the southern end of the stream (cf. Pl. I, phot. 2). The vegetation is breast high and is predominantly dense hummocks of *Molinia* with bog myrtle, rushes and here and there *Osmunda*; over the top of this trail bramble (*Rubus*) and honeysuckle (*Lonicera*). Such areas are difficult to pass through and they were only tested at intervals to determine the penetration of *Conocephalus dorsalis* (Latr.), and to make certain that *Mecostethus grossus* (L.) was not present.

(5) *Marshy spots and damp hollows.* The plant communities included under this group are rather varied. On the flat surface of Plateau Heath there are moist patches where the predominant *Calluna* gives way to *Erica* with some *Drosera* and tufts of *Leucobryum* and *Sphagnum*; occasionally fine grass is intermingled. This grass becomes more prevalent along the ruts of old cart-tracks. There are several shallow, circular hollows (presumably artificial) (Pl. II, phot. 3). In these grass predominates and in 1931 standing water was invariably present (in a dry year they are quite dry). The marshy spots off the plateau are somewhat different; they are found only in natural depressions, most of which lie in the area between the road and the stream. Generally they are disconnected elongate strips running north and south. In their least

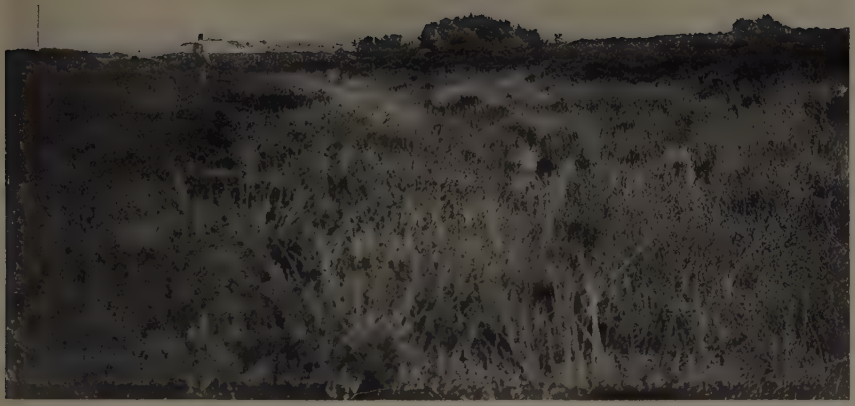


Photo. E. J. H. Edenborough, May, 1932

Phot. 1. A typical marshy depression (*Molinia, Myrica, Juncus*) in the heather of Third Ridge, looking north; sallow and birch clumps in the middle distance.

Photo. E. J. H. Edenborough, May, 1932

Phot. 2. Swamp (*Molinia, Myrica, Juncus*) between Little Sea and Eastern Lake, looking north; often breast high and with several inches of standing water.

pronounced form they are quite small dips with slightly damp grassy bottoms. In the longer and wetter hollows tussocks of grass and bog myrtle appear with occasional rushes (Pl. I, phot. 1), and the community becomes similar to that described above for the marshy extensions of One-acre Pool. Two or three of these depressions are occupied by clumps of sallow and birch (see middle distance in Pl. I, phot. 1) under which, of course, a totally different flora is to be found, but since such spots are not occupied by Orthoptera they need not be described in detail here.

Whereas near the road it is correct to speak of moist depressions in the surrounding heather-covered ground, towards the stream it is more correct to speak of elongate islands of heather rising slightly above the general level. Here the soil surface of the general level is not wet, but is inclined to be moist. It is mostly covered with moderately tall grasses, bog myrtle and occasional patches of rushes; in the more open spots heather appears. The vegetation is not dense and seldom reaches above knee height. Towards the south, there is an open marsh largely occupied by tussocks of grass and deep cushions of *Sphagnum*. Most of the actual soil surface here is under water, and towards the centre there was, in 1931, a patch of open water ("New Pool").

On the eastern side of the stream conditions are a little different. Second Ridge and its spurs in many places pass abruptly into dense marsh; but, here and there, there are flat strips and tongues, upon which short bog myrtle, grasses, rushes and *Erica* grow.

(6) *Bordering heather*. The distinguishing feature of this locus type is that it is an open community. Although heather is the predominant plant, it is not the only one; and further the clumps are only a few inches in height. Between these scattered clumps are patches of lichen, moss and open sand; fine short grasses grow intermixed with these. There is also the distinction that this type of locus carries a definite orthopteran population, whereas the tracts of pure *Calluna* do not.

(7) *The ridges*. The vegetation of Second and Third Ridges is simple. Near the north-east shore-line the sand is more mobile, being fixed only by occasional tufts of *Psamma*. On Secondary Ridge this rapidly gives way to pure heather. On the shorter ridges that just come into the northern boundary of our area, and on either side of Northern Enclosure, the marram gives way to gorse with short grasses and only occasional heather; here some ragwort (*Senecio Jacobaea*) grows in the hollows. There is nothing corresponding to the landward slope of First Ridge.

(8) *The plateau*. There is a marked contrast between the heather of the ridges and that of Plateau Heath. The former is high well-grown clumps of *Calluna* rising from dry sand, while the latter is short with a considerable proportion of *Erica* growing from a black soil with a marked tendency to a damp surface and wet patches ((5) above) (see Pl. II, phot. 3). The visible

effects of the change from blown sand to the exposed Bagshot beds is quite striking. Generally speaking, as the ground drops away to the harbour shore the clumps of *Calluna* become deeper, some bracken appears and the community gives way to a fringe of gorse bushes. Similarly, the *Calluna* becomes deeper as Curlew Heath slopes to Little Sea, and south of Curlew Cottages there is much bracken and some pine trees.

(9) *The plateau enclosure.* This flat strip of nearly 4 acres, enclosed by a low bank, preserves the general level of the plateau (about 20 ft.) except where it slopes steeply down to the margin of the lake. The southern end and its slope are covered with bracken, gorse and bramble, but the major part of the area is covered with short grass, ragwort and low bramble bushes (Pl. II, phot. 4). There are some stunted sallows and a clump of trees on the slope down to the lake.

(10) *The roadside.* This, naturally, does not provide an entirely homogeneous locus. Sometimes the road cuts through pure heather leaving bare sand margins, but on the whole it provides a narrow margin of short grass with small patches of exposed sand running into the heather. Occasionally the strip widens and longer grasses and ragwort are present; in parts there are drainage ditches with a moist bottom.

(11) *The harbour shore.* Similarly, there is some variation in the harbour shore. Except in the small inlets, the actual shore-line rises 2 or 3 ft. above the beach and generally is fringed with gorse or heather. Down to the beginning of Bramble Bush Bay the beach is more or less sandy with some short grass growing here and there about the high-tide mark. There are one or two small grassy dips that run into the heather. In this bay the Bagshot beds first appear with the clay, mud and pebbles that form the remainder of the shore-line. Strips of short beach grass and patches of rushes occur at intervals along the rest of the shore. In Bramble Bush Bay and in the bay south of it ("Dyke Bay") there are wider grassy margins and saltings with rushes just above the tide mark and sea lavender (*Statice Limonium*) just below; further out there are large clumps of *Spartina*. Round Jerry's Point there is *Spartina* below the tide mark and close short grass above. Redhorn Quay is similarly covered with short grass and a few plants of ragwort are established.

Northern Enclosure (*alluvium*). Just beyond the northern boundary of the area, where the stream runs out into the sand, there is a wide patch of saltings composed of rushes and grass. This is cut across by the bank of Northern Enclosure, but continues for some way within the enclosure on both sides of the stream. The ground here is definitely wet, but towards the west and south becomes drier and a grass community takes the place of the rushes and continues up to the western bank. Southwards again this community changes to one of tall grasses, bog myrtle and a bush or two of gorse. This again gives way to lower herbage with *Erica* and occasional *Calluna* which continues

until the southern bank is reached. These banks, and those on either side of the stream as it leaves the enclosure, carry high grasses with some bramble, and on the western side gorse. Bog myrtle and rushes grow in the ditches. Northern Enclosure has not been included independently among the locus types because of its varied nature. Its area is approximately 6 acres.

(*Note.* The area was under observation during the whole of the very dry summer of 1932. Though by the end of May there was no striking difference in the water-level observed during the previous August, by August of this year the general level had dropped by about a foot, leaving, for instance, the circles on Plateau Heath quite dry. Eastern Lake shrank very considerably and large areas of its floor were exposed; nowhere within its margins could it be said that there was open water. The effect on Little Sea was less obvious; but the swamp vegetation was lower, its floor drier and penetration consequently was far less arduous. The large dragonfly, *Libellula quadrimaculata*, was seen in mid-June laying freely in the foot-deep water of the open grassy marsh to the south of Eastern Lake. By September there was no water here at all.)

IV. The species found.

Ten species representing four orthopteran families were found in the area. (In August, 1932, *Ectobius pallidus* (L.) (= *perspicillaris* Herbst.), a species we had expected to find, was added. It was taken from the marram tufts on Second and Third Ridges.)

(1)	Blattidae.	*Ectobius panzeri* (Stephens).
(2)	Tettigoniidae.	*Metrioptera brachyptera* (L.).
(3)		*Conocephalus dorsalis* (Latreille).
(4)	Acrididae.	*Omocestus viridulus* (L.).
(5)		*Myrmeleotettix maculatus* (Thunberg).
(6)		*Chorthippus* (*Stauroderus*) *bicolor* (L.).
(7)		*Chorthippus* (*Stauroderus*) *parallelus* (Zetterstedt).
(8)		*Chorthippus* (*Chorthippus*) *albomarginatus* (De Geer) (= *elegans* Charp.).
(9)	Tetrigidae.	*Acrydium subulatum* (L.).
(10)		*Acrydium kiefferi* (Saulcy). (British representatives of this species were previously referred to *A. bipunctatum* which, according to Uvarov (**3**), has not yet been shown to be a member of the British fauna.)

The detailed distribution of the cockroaches was not worked out, our attention being confined to the three families of grasshoppers, but *Ectobius panzeri* was taken from several places within the area. Lucas (**1**) also records it from here. Our specimens were taken from type (6) loci, where short heather grows mixed with low grasses leaving some exposed sand; and freely, at night (1932), on the marram tufts of First and Second Ridges (type (1)).

V. Methods.

The Ordnance Survey (1925 edition), scale 25·344 in. to the mile, was traced on to inch-squared paper and then divided up into 2 in. squares which were numbered consecutively. Thus the side of each large square measured 139 yards and its area approximately 4 acres. As far as conditions and time would allow, the fauna of the different plant communities in each sub-square (= each acre) was examined and the results recorded in a field note-book under the square number. The records thus rest primarily on inspection of the living insects, but a number of specimens also was taken.

Following our success, in 1930, in sweeping *albomarginatus*, we had intended to rely mainly on this method for our population samples, using detachable sweep bags so that each sample could be kept separate. It at once became apparent that this method, though possible for species that rest up in the plants (e.g. *dorsalis*), was quite ineffective for our general purposes, and we had to resort to the more laborious method of taking samples by hand. Each sample was collected into an oblong bag made from a 9 in. square of "balloon cloth" and fitted with double tape drawstrings at the mouth; when the sample was completed the mouth of the bag was drawn tight and the whole bag put into a large cyanide bottle. (Chloroform is unsuitable as it changes the green coloration to red.) While collecting, the mouth was kept sufficiently drawn up to allow the easy insertion of new specimens without those already inside being able to escape. Although this may sound a difficult operation with insects as active as grasshoppers, in practice it proved quite simple. In uniformly low vegetation ground sweeping was found to be effective, at least for Tetrigids.

VI. The general grasshopper population.

A rough measure of the degree of occupation may be obtained from the number of species recorded from each square.

The area was divided into 141 squares, but of these some were "non-effective" in that they contained no habitable land (e.g. only sea-beach sand). When these are eliminated there remain 122 "effective" squares, of which 94 or 77 per cent. are "occupied" by at least one species of grasshopper. The number of square records for each species, in order of decreasing frequency, is

Myrmeleotettix maculatus	55
Acrydium kiefferi	53
Chorthippus bicolor	48
Metrioptera brachyptera	45
Chorthippus parallelus	42
Conocephalus dorsalis	40
Acrydium subulatum	10
Chorthippus albomarginatus...	5
Omocestus viridulus	2
Total records	300

(When a colony cuts into the borders of more than one square it must logically be recorded as present in each of the squares.) Two distinct groups appear, the "common" group containing six species and the "rare" group containing three. The terms "common" and "rare" are used here purely in relation to this area, and not to the general distribution of the species. In Wicken Fen, for instance (Lucas (**2**)), our three "rares" together with *dorsalis* are the only species reported as present. Undoubtedly the figures for some species could have been increased had more time been available, but in any case such figures cannot be taken as more than a rough guide to the relative frequencies.

The frequency distribution of the squares in terms of the number of species per square is:

No. of species per square	0	1	2	3	4	5	6	7	8	9	Total
No. of squares	28	14	19	28	11	13	9	.	.	.	122
Per cent.	23	11	16	23	9	11	7	.	.	.	100

The absence of squares with as many as eight or nine species is due to the fact that two of the "rares" have a distribution restricted to the relatively unpopulated northern part of the area. If the spring record for *subulatum* were included, there would be one square near One-acre Pool with all the remaining seven species recorded; and others in Bramble Bush Bay, but for the thinness of the *maculatus* population. The averages for the whole area are, per "effective" square 2·5 species, and per "occupied" square 3·2. The natural conclusion from these figures is that if a locus is habitable it is usually occupied by several species.

A better idea of the relative concentration of population can be obtained by dividing the area up into well-defined sub-areas. These divisions do not coincide with the arbitrary squares, consequently it has been necessary to count twice those squares that fall across natural divisions and to dissect the total of the records for the square; for instance, in the square that embraces the northern tip of Little Sea, a total of five species is recorded, but part of this square belongs to the Bagshot beds, and upon that part three species were recorded, while the other part belongs to the south-central sub-area and three species were recorded here; that is, one species was recorded in both parts of the square, while of the other four, two were confined to one part, and two to the other.

(i) The Bagshot beds (locus types: (8), (9), (10) and (11)). Forty-four effective squares of which 13 or 30 per cent. are unpopulated. The total of the records for these squares is 89, an average of 2·0 species per square; but of these 89 records, 38, or 43 per cent., are concentrated in seven atypical squares, of which three are on the shore of Bramble Bush Bay where there is practically no population behind the actual shore, and four involve the road side and Plateau Enclosure. These seven squares have an average of 5·4 species per square, while the remaining 37 squares have only 51 records or 1·4 per square.

(ii) South-central: lying between Little Sea and Saltings Strip (locus types: mainly (4) and (7), and some (5) and (6)). This embraces the densest part of Central Marsh and two strips of heather. It includes 23 squares and 26 records, or an average of 1·1 species per square. There are three squares with three records each, resulting from one small colony (*bicolor*, *maculatus*, *kiefferi*) which happens just to cut into all the three squares: except for this colony these squares were recorded as barren.

(iii) North-central: from the edge of the Bagshot beds to Saltings Strip, and in the north excluding the four shore squares of which three are unpopulated dune (locus types: (5) predominates with (6), (7), (9), (10) and (11) represented). This area embraces 32 squares, or parts of squares, and 114 records or 3·6 species per square. There were only two unpopulated squares which are covered with the pure heather of Second Ridge.

(iv) Saltings Strip and First Ridge: including Eastern Lake and its marshes (locus types: (1), (2), (3) and (6)). This covers 24 squares with a total of 80 records or 3·3 species per square. Two squares which were under standing water were uninhabited.

The real centre of population is the system made up by Bramble Bush Bay, Plateau Enclosure, the One-acre Pool marshes, and so much of the roadside as runs through it (see Text-figs. 3 and 4) (locus types: (5), (6), (9), (10) and (11)). This area is roughly square embracing 17 squares, one of which being pure plateau heath is unpopulated and may properly be excluded. For the 16 squares there are 86 records or 5·4 species per square. This is outside the range of the two "rare" northern species and has only three records for *subulatum*. If these are subtracted, we are left with 83 out of a possible total, for the six "common" species, of 96 records, which gives the extraordinarily high figure of 87 per cent. occupation. The corresponding figure for the whole area, that is, subtracting from the total the 17 records for the three "rare" species, is 283 records with a possible total of 732 or 39 per cent. occupation.

On the other side of the picture, the percentage of occupation for the plateau itself (8) (see Pl. II, phot. 3), that is, excluding the records of species confined to the lake-shore marshes, the roadside and the shore, is only 12 per cent. or about 0·7 of a record per square. The southern end of Central Marsh (4), where the vegetation was extremely dense and breast high (see Pl. I, phot. 2), was admittedly only penetrated by us here and there; but our results, which give a figure of about 3 per cent. occupation, probably are not far from the truth.

VII. Problems of distribution.

The distribution of a species may be considered in relation to (*a*) geographical space, (*b*) types of habitat, or (*c*) population intensity. A species that ranges through the Palaearctic region may properly be said to have a wide distribution in the geographical sense, but it may have a very restricted

distribution in respect to the type of habitat that it can occupy, and it may be even further limited in that it does not in fact occupy all those areas in which its particular habitat is available. In an enquiry of this nature, where the area under consideration is very limited, it is not easy to assess the facts in terms of these three distinct sets of problems. The geographical aspect might be involved in the case of a species that has a "continuous" distribution (in the sense that it occupies all, or practically all, the suitable spots) within part of an area, but that does not extend to any of the suitable spots outside a particular boundary. But if there be no obvious barrier to the further spread of the species, it would not be safe to assume, without careful enquiry, that the apparently suitable spots outside the boundary were in fact the same in all essential respects as those within it. The distribution of *parallelus* (p. 53) affords a good example of this type of problem.

VIII. Recent physiographical changes.

The solution of small-scale problems of "geographical" spread cannot proceed far without some knowledge of the recent history of the area. In this case rapid changes have taken place in the last 200 years (C. Diver, in press) which have had the effect of limiting the distribution of some species while increasing the potential spread of others. Old barriers have disappeared and new ones have arisen. Several of the locus types are of quite recent origin; for instance, in 1849 high water covered Saltings Strip and reached Little Sea, and First Ridge was a low sand bar covered at exceptional high tides. In 1894, the floor of Eastern Lake was a direct continuation of the beach and was labelled "flooded sand (salt)"; One-acre Pool did not exist. By 1900, both these lakes had formed. Practically the whole development of Central Marsh took place between 1900 and 1925 (Text-fig. 2).

When a habitat changes, the faunal response is fairly rapid; the old species disappear and more suitable ones, if near at hand and not cut off by physical barriers, soon colonise the new territory. An example of this is the roadside which now carries its distinctive and fairly numerous population, though it has only existed as a locus for five or six years. But these problems cannot well be discussed apart from the facts relating to the ranges of habitat that different species will tolerate.

IX. The distribution of the species in relation to habitat type and "geographical" spread.

In this section it will be more convenient to consider the species in groups related to the facts of distribution and the problems presented, rather than in their taxonomic order. An obvious grouping is:

(*a*) Absentees. The problem here is why certain species, that might be expected, are not present.

(*a*) 1886 (*b*) 1900 (*c*) 1924

Text-fig. 2.

(*b*) Species of limited distribution. This cuts across the grouping into "common" and "rare," for *subulatum*, though rare, has a wide geographic extent and *parallelus*, though common, has a limited area of occupation.

(*c*) Species of wider distribution.

(*a*) *Absentees.*

Among the Tettigoniidae, *Tettigonia viridissima* (L.) might have been expected in the grassy area of Plateau Enclosure, as it occurs in the neighbourhood, at Lilliput in the north and "near Swanage" in the south. In 1932 this species was recorded by Dr P. A. Buxton from two loci in the neighbourhood of Studland, and was heard by one of us in the gorse bushes near Pipley Bridge, about a mile to the south of the area surveyed. Dr Buxton also took, at light, in Studland village a specimen of *Meconema thalassinum* (F.). This tree-living species may occupy some of the southern part of South Haven Peninsula, but it is doubtful whether it will be found within our area. Among the Acrididae, *Mecostethus grossus* (L.) has been taken, according to Lucas' description (**1**), in conditions like those now obtaining in Central Marsh. It was recorded in 1880 from "Dorset heaths and the Isle of Purbeck" (Lucas (**1**)), but we did not find it within our area. The species was taken in August, 1932, by Dr P. A. Buxton and again by Dr Buxton and ourselves from two boggy heaths a few miles to the west. These loci were open *Sphagnum* bogs with uniformly low vegetation quite unlike Central Marsh. Such conditions do not occur in the area now under consideration.

(*b*) *Species of limited distribution.*

All the three species that fall into this group belong to the Acrididae.

O. viridulus (Text-fig. 3).

Only two examples of this species were taken. One in the tall grass on the bank of the stream near where it enters Northern Enclosure; the other in equally tall dense grass some 140 yards west near the south-west bank of the enclosure, where also there is a water-filled ditch. The banks themselves were not carefully examined owing to the difficulty of getting at them, and it may be that this species maintains a precarious existence on them. The species was not found within this enclosure, possibly because the grass there was not

---

Text-fig. 2. Three maps based upon the Ordnance Survey Maps of (*a*) 1886, (*b*) 1900 and (*c*) 1924, with the sanction of the Controller of H.M. Stationery Office, showing the changes that have taken place during this period of 38 years. Each map shows identically the same strip of country. Note: (1) the growth of the saltings in Bramble Bush Bay; (2) the appearance and growth of One-acre Pool and its surrounding marsh; (3) the appearance and growth of Central Marsh; (4) the appearance of and changes in Eastern Lake; (5) the development of marsh in the extreme south; (6) the building up of First Ridge; (7) the seaward advance of the coast-line.

sufficiently high and lush. Lucas, who from his records (1) had clearly worked in the Studland area, gives no Dorset record for this species (the nearest being the New Forest), so, obviously, the species is not a common one in the surrounding district. We, however, found it at Corfe (p. 68). Of its general habitat Lucas says "on the whole perhaps it affects slightly elevated grasslands, moors and similar places more frequently than low-lying spots, though Morley records it from marshes." Where we took it the ground is not more than a foot or so above sea-level. Though recorded as present in Wicken Fen, Lucas (2) says "it does not seem specially associated with wet places."

The distribution on South Haven Peninsula presents two problems. First, is its limitation due to the absence of other suitable loci, or to the animal's failure to reach such as may exist? Unfortunately we do not yet know enough of this grasshopper's habits to offer an answer to this question. Secondly, how did the species reach its present isolated locus? This question is open to two types of answer:

(i) That it once had a wider distribution from which it has been driven by encroaching heather. About this we have no evidence either way.

(ii) That it has transported itself, or been transported, across the water from Sandbanks, which necessitates the improbable assumption that it once had a footing there, or from Branksea Island, which we have not yet examined, or across several miles of heath from somewhere in the Studland or Corfe Area (involuntarily, perhaps, in hay brought to the old cottage near South Haven Point).

C. albomarginatus (Text-fig. 3).

This species is plentiful, though patchy, in the saltings north of Northern Enclosure (just beyond our boundary), where it is the only species and occupies the rushes and tall grass up to the open sand. Within Northern Enclosure it is also present on the drier grassy parts with *bicolor*, but not with *dorsalis* among the more or less flooded rushes. Some 150 yards east, in a narrow grassy strip between two dunes, one specimen was taken with two *bicolor* and one *brachyptera*. At the northern end of Saltings Strip the species occurred in the north-eastern tongue, accompanied by *dorsalis* and the two Tetrigids, but it does not appear to be established in the main body of the strip. It was not found elsewhere in our area.

The early maps suggest that the area round Northern Enclosure may have been a suitable habitat for this species for at least 200 years. But, though the main Saltings Strip developed between 1850 and 1886, its north-eastern tongue is not thirty years old. The population here is thin, the remains perhaps of a more continuous population along the north-east coast during the '70's of last century, or the product of wanderers which had crossed some 450 yards of mostly unsuitable country. If capable of this, why then has the species not established a population in the saltings of Bramble Bush Bay, only some

500 yards to the south-west of Northern Enclosure? If this absence is not accidental, the only suggestion we can offer is that, although the species can live on alluvium or sand, it does not care to do so on the clay of the bays.

A flourishing colony (now largely obliterated by the construction of a new pier and car park) existed in 1930 on the harbour shore near Lilliput in the rallish grass just above high-tide mark: but at least part of this area was liable to flooding by exceptional tides. The surface conditions here do not appear very different from those in the two bays.

The records given by Lucas (1) indicate that the usual habitats are damp grassy spots and marshes and that the species is predominantly, though by no means exclusively, coastal in its distribution. Lucas states "it is quite as frequently reported from sandhills," but it is not clear whether it actually occupies the dunes or whether it has been found only, as here, in the damp "slacks" behind the ridges. The nearest Dorset locality given is as far away as Weymouth, but the species will no doubt be found in other places round Poole Harbour.

C. parallelus (Text-fig. 3).

Of this species Lucas (1) says "meadows and open ground constitute the usual habitat of this very common grasshopper. Possibly it prefers ground that is inclined to be damp rather than too dry."

Its main distribution on South Haven Peninsula is over the area of the exposed Bagshot beds. From this a narrow tongue of population, through the centre of which runs the road, extends almost to our northern boundary. Thus in the southern half, with one exception, the western shore of Little Sea forms its eastern boundary; while in the northern half the species does not extend further than some 300 yards east of the road, and nowhere penetrates the borders of the dense part of Central Marsh. This curiously limited distribution might suggest that the species, owing to its winglessness, does not spread with ease; yet throughout the country at large it is well distributed and "very common."

In the north the species was found in one or two of the grassy dips in Third Ridge; near the banks of Northern Enclosure (but it does not appear to have colonised any part of the enclosure itself, though this seems suitable ground); in several marshy hollows between the road and the line of the willow clumps (Pl. I, phot. 1); round the marshy edges on both sides of One-more Pool (on the east side it forms about 19 per cent. of the grasshopper population, 7 out of a total sample of 36; on the west side 13 out of 64, or about 20 per cent., see p. 47); in the grassy margins of the marsh bordering the northern tip of Little Sea (a few only); and in several grassy spots between One-more Pool and the harbour shore. These are all type 5a (not on sand). Along the roadside (10) it was not seen for the first 450 yards, but was found along the next 700 yards as far as "Plateau Dyke"; along the 700 yards

between the two dykes it was not found, though present in the heather on either side; south of "Curlew Dyke" the roadside population starts again and continues for the next 200 yards to our southern boundary.

Though it has not occupied the damper grass of Northern Enclosure (alluvium) it has colonised the well-drained grass of Plateau Enclosure (partly sand and partly Bagshot beds) (Pl. II, phot. 4), where it forms about 11 per cent., 8 out of 73, of the total grasshopper population. On the harbour shore (11) it was not found for the first 450 yards, but was present at the back of the saltings all round Bramble Bush Bay (partly sand and partly clay); the distribution stops short of Jerry's Point and only begins again some 500 yards south behind the saltings on the clay of Dyke Bay. (In August, 1932, the species was recorded from the shore half-way between Jerry's Point and Dyke Bay.) This population, occupying a strip of about 200 yards, is connected with the roadside by a scattered population along the sides of Plateau Dyke; from the rest of the shore it was not recorded.

Apart from a few isolated *brachyptera* and *maculatus* that have strayed from the shore of Bramble Bush Bay or the roadside, there are no grasshoppers on Plateau Heath except *parallelus*. The shallow circular hollows (above, p. 40) always contain a certain amount of grass. In some, the floor was completely covered with an inch or so of water, these were not usually occupied (Pl. II, phot. 3); but in others the standing water was limited in extent and *parallelus* was generally present. The species is also present in the other moist patches where there is a sufficiency of grass; along the sides of both the dykes; and along the old cart-tracks in the south. In view of this, it is somewhat curious that this species was not taken with *bicolor* along the shore on either side of Redhorn Quay; it may, however, have been missed here, as this area had to be rather hurriedly worked. (In August, 1932, it was taken in the small inlet on the shore just south-east of Redhorn Quay.) It was taken with *bicolor* in the marsh immediately round the point of the lake by Curlew Cottages, and south of this with *brachyptera* round the tip of the western extension. On Curlew Heath it occurs sporadically, mostly between the road and the footpath and towards the enclosure end, where the ground is flatter and less well drained.

The only colony outside these limits is a small one spread out for some 200 yards along the narrow strip of low grassy heather (type (6) merging into type (5)) which divides Eastern Lake from the open marsh on the southern border of our area. The species was noted by one of us at the northern end of Saltings Strip, but no specimens were taken in the samples from there, and it is quite likely that a male *albomarginatus* was mistaken for it. It may therefore be regarded as absent from the marram dunes (1), the saltings (2), the lakes (3), swamp (4), most bordering heather (6) and the heather ridges (7).

To sum up, its typical locus is (5), it is present in types (8), (9), (10) and (11), and it alone seems able to stand the conditions of Plateau Heath.

Photo. E. J. H. Edenborough, May, 1932

Phot. 3. One of the artificial "circles" (*Molinia, Scirpus palustris, Carex panicea*) on Plateau Heath, looking north-west; the gorse fringe of the harbour shore in the middle distance.

Photo. E. J. H. Edenborough, May, 1932

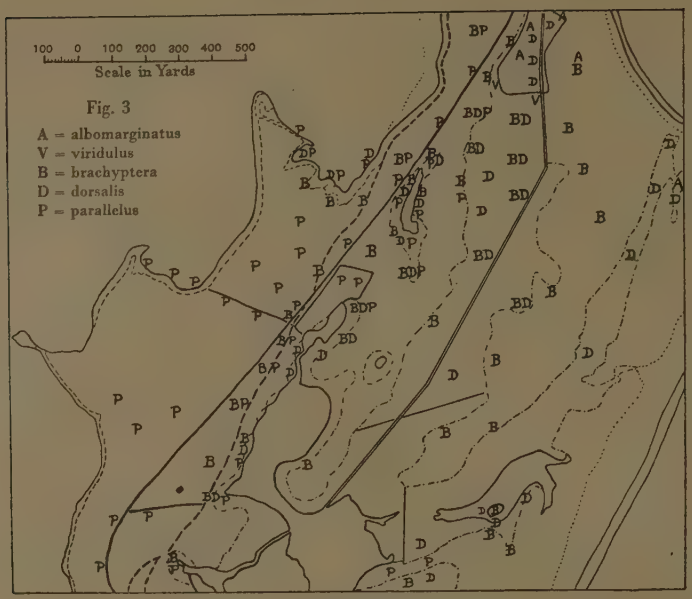
Phot. 4. Plateau Enclosure (grasses, bramble bushes, etc.), looking north-east; Third Ridge in the background.

This restricted distribution does not appear to result from the absence of suitable loci outside its limits. What, therefore, are the barriers? To-day, the stream with its belt of presumably uninhabitable marsh provides an obvious barrier to any eastward spread; but the marsh did not exist in 1900 and the stream had not been cut by 1849. At this recent date the species might have wandered right up to the present edge of Saltings Strip, had the country been suitable, but the evidence suggests that, except for the southern end of Central Marsh, it was then dry and sandy. Apart from the improved amenities resulting from the construction of the shallow circles, the dykes and the expansion of the shore saltings, there is nothing to lead us to suppose that the conditions on the plateau have altered much in the last 200 years; but in the area now covered by the northern tongue of population there have been considerable and quite recent changes. The marshy borders of One-acre Pool are not 40 years old; others of the type (5) loci are less than 30; while the roadside is about six. From this information we may fairly deduce that the species has long been established on the plateau, and that in the past it was confined to this area by the absence of other suitable loci. The spread on to the sand was made possible somewhere about 1900 as the area became wetter, and has no doubt been helped more recently by the construction of the road. But during this time the development of Central Marsh was proceeding, and a new barrier, more effective than the stream, was being created. In time, if conditions do not become more unsuitable, the species may penetrate Northern Enclosure and thus perhaps reach a few loci east of the stream, for it can, and elsewhere does, live with *albomarginatus* and *bicolor*.

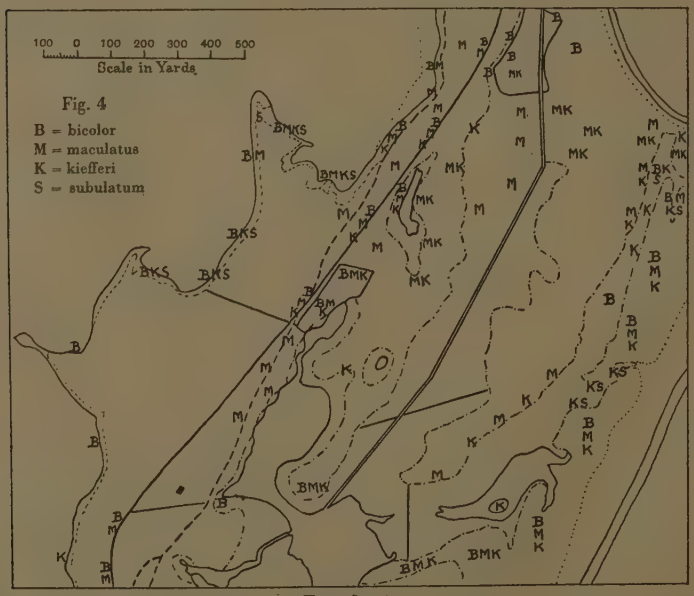
The isolated population in the south cannot usefully be discussed until the conditions beyond our present boundary are known, but it might provide a starting-point for the colonisation of some of the more suitable spots round the eastern edge of Saltings Strip. (Dr Buxton's and our own records during 1932 from the area immediately south of our present boundary show that the species is well established in suitable spots east of Little Sea, and that this population represents the present northern end of its range on this side of the lake.)

(*c*) *Species of wider distribution.*

This group includes six species, the two Tettigoniids, the two Tetrigids and the two remaining Acridids. The Tetrigid, *subulatum*, belongs to the "rare" group, the other five species are "common." The two Tettigoniids and *subulatum* belong to the group inhabiting damp loci, while *bicolor*, *maculatus* and *kiefferi* are more tolerant and form the usual dry community (see Table II). It is more convenient, however, to consider *subulatum* with its congener *kiefferi*, as in this area the former has not been found apart from the latter, and the Tetrigids as a group present somewhat different problems



Text-fig. 3.



Text-fig. 4.

Text-figs. 3 and 4. The surveyed area of South Haven Peninsula showing the distributions of the nine species of grasshoppers, as recorded in August, 1931. Based upon the Ordnance Survey Map, with the sanction of the Controller of H.M. Stationery Office.

from the others. Three of the "common" species are without functional wings.

C. dorsalis (Text-fig. 3).

We are informed by Mr Uvarov that this species lays its eggs in the stems of *Juncus*. The association of this animal with a species of *Juncus* was noted in Wicken Fen (Lucas (**2**)). Although we took it off patches of bog myrtle and grass tufts where there were practically no rushes, we did not find the species in any place where rushes were definitely absent. (In August, 1932, we took about six from a grassy patch where the only *Juncus* within range was a single well-developed plant of *J. communis* 15 yards distant, round which, incidentally, no *dorsalis* was found.) Consequently it was recorded only in marshy spots, locus types (2), (3), (4), (5) and (11). On the other hand, the presence of rushes does not necessarily imply the presence of *dorsalis*.

Though neither this species nor *brachyptera* is adapted for flight, there is an interesting difference in their distributions. The latter is generally, though not thickly, distributed over the area it occupies, but *dorsalis* was found to be definitely patchy in areas where continuity might be expected, a fact well exemplified in Saltings Strip. At the northern tip of this strip rushes begin on the flat dryish sand and continue southward over ground that is getting slowly but steadily wetter, until it imperceptibly becomes the floor of Eastern Lake. The species was taken quite close to the tip, and was found patchily for the next 800 yards southwards. Beyond this the soil surface in the centre was definitely under water. By wading, a rough survey was made of the southern end of the strip and the lake itself. *Dorsalis* was seen in three places only, all within the present margins of the lake: in loose clumps of rushes near the island shore; half-way between the island and the southern shore; and near the southern shore. The occupation of these loci in a wet year could only be accomplished by a considerable swim (Pl. III, phot. 5). The breast-high vegetation towards the dyke (see Text-fig. 1 and Pl. I, phot. 2) was penetrated in several places from the shore and from the lake, but except for one small patch near the dyke nothing was found.

In the open grassy marsh on the southern boundary—a typical locus for *brachyptera* from which *dorsalis* would be absent—we found in one spot a few spikes of rush and round these were three or four *dorsalis*.

At its southern end Central Marsh is wide and its vegetation is dense. This character is preserved with a slight diminution of width for some 700 yards northwards. Penetration was effected in several places on both sides of the stream and only once was *dorsalis* recorded; the margins were equally unpopulated. The width of the really dense marsh now rapidly decreases, its place being taken by lower vegetation which allows the better development of rushes, and the population of *dorsalis* begins. From here to Northern Enclosure, between the stream and the road, the species may be found in

most of the marshy areas and damp hollows (Pl. I, phot. 1). On the eastern side of the stream there is little low marsh and none after the stream turns due north; consequently the species was only taken in one or two spots. In the *Juncus* beds of Northern Enclosure, although still noticeably patchy, *dorsalis* was reasonably plentiful. Perhaps the most continuous population found was that round One-acre Pool: in some 2 acres of this marsh about 50 individuals were seen.

Along the length of the harbour shore there are occasional strips of rushes, which are most developed in, though not confined to, the two bays. *Dorsalis* was found all round the shore of Bramble Bush Bay which is close to its main distribution, but not in the similar shore loci south of this. (In August, 1932, it was recorded from the shore half-way between Jerry's Point and Dyke Bay.) It occupies the rushes growing about the high-tide mark, but is absent from the *Spartina* growing between the tide marks. Lucas (**1**) refers to a possible association between this species and sea lavender (*Statice*); although this plant was present in both bays, no such association was observed.

On the plateau there is no suitable habitat.

To sum up: The species appears unconcerned as to whether the soil surface is comparatively dry or covered with water; it prefers the more open, shorter vegetation to that of the main body of Central Marsh, though occasionally it is to be found in the more suitable parts of this. Within these limits there are practically no extensive patches of rush which have not been colonised at least in part (though in the north-central area many must be of recent origin), and several are separated from the nearest population by as much as 100 yards of uninhabitable heath. The only notable exceptions to this are the two strips on the harbour shore, one in Dyke Bay and the other some 500 yards south of Redhorn Quay. These are separated from the nearest populations by 500 and 400 yards respectively of plateau heath. It would, therefore, seem that this distance of thoroughly unsuitable country may form an effective barrier to distribution.

M. brachyptera (Text-fig. 3).

The main distribution of this species lies within a wide central belt running the length of the area. Within its limits, *brachyptera* was present in nearly every small marsh and damp hollow (Pl. I, phot. 1). It is freely distributed in the more open vegetation in the northern half of Central Marsh and in several suitable spots on the borders of the swamp, but it does not penetrate really dense vegetation; it is similarly distributed round the marshy borders of the lakes; and it has occupied the roadside and other ditches. It was sometimes found in the drier heather of types (6) and (7); and was present on the island in Eastern Lake (Pl. III, phot. 5), where possibly it was marooned sometime during the last 35 years (in a very dry year it might reach this without swimming).

It was not found in the marram dunes (1), in the saltings (2), on the rushes in the lake (3), in swamp (4), or established in the heather ridges (7). It was apparently absent from Plateau Heath (8), though several spots had all the outward appearances of suitable loci; it is, however, present on the Bagshot beds along the roadside ditches, and on Curlew Heath. It was absent from Plateau Enclosure (9), although present in the heather, marshes and ditches on all sides of it; similarly it occurs on three sides of Northern Enclosure but does not enter it. With the exception of one small patch in Bramble Bush Bay, where it was found behind, not in, the saltings, it was absent from the harbour shore (11).

On South Haven Peninsula, then, its typical locus is (5). It occurs where the vegetation is quite low up to where it is about knee high; it does not appear to like very dense vegetation or places where the surface is always slightly under water. Its absence from Saltings Strip and Plateau Heath requires other explanations. It can apparently stand a drier surface if the vegetation is reasonably high, and we did, in fact, find the species in such a locus near Lilliput (tufts of high grass on the flat top of a 6 ft. bank above a partially dried stream bed).

Lucas (1) states that in his experience the species "inhabits heathy ground, but affects by preference moist spots or even the surface of bogs."

The species walks vigorously, which may account for its less patchy distribution. Its colonisation of a little grassy dip isolated in the middle of Second Ridge indicates that it can wander over pure heather for distances as great as 200 yards.

With these powers of spreading, it does not seem likely that its absence from Saltings Strip and its borders can be ascribed to its inability to reach these areas. It is surprising that it was not recorded from the borders at the southern end of the strip; but it may be that here the change from the dry short bordering heather to the dense tall vegetation of the marsh is too abrupt to allow a niche suitable for the occupation of this species. (In August, 1932, one specimen was seen on the eastern border just south of the central tongue.) It seems plain that for some reason it does not thrive in rush saltings; but quite clearly it is not the presence of the rushes that it objects to.

The absence of this species from the flat damp surface of Plateau Heath is also surprising, as it is present on the drier and slightly sloping parts of Curlew Heath. We can only suggest that undrained clay is not suitable for its development, though it can live on the almost floating mat of low vegetation that forms the surface of a bog.

The distributions of this and the last species overlap considerably, but the one is not included in the other. *Dorsalis* cannot follow *brachyptera* into open marshes and damp hollows with no rushes, and *brachyptera* does not follow *dorsalis* into high herbage or standing water.

During the last 30 years, while Central Marsh has been developing, there

must have been an interesting northward shift of both these species, for both can occupy the early stages in the making of a marsh, but neither the later stage of breast-high swamp. The area suitable to them in the north-centre must have increased rapidly in recent years.

Both species were absent from the marsh round New Pool (p. 41).

C. bicolor (Text-fig. 4).

This species is absent from really wet situations ((3) and (4)), but is apparently more tolerant of dampness than *maculatus*, as it has penetrated the less water-logged parts of Saltings Strip (2) in several places. On the other hand, though found where heather is growing among grasses and other plants (as at the foot of the dunes), it does not follow *maculatus* into areas where heather is predominant. Nor does it often follow *parallelus* into type (5) loci. It occurs, though not plentifully, along the whole of the landward slope of the dunes ((1) and (6)) (Pl. III, phot. 6) and continues round the southern side of Eastern Lake until the bordering heather gives out; but it is not so frequent nor does it press so near the shore as *maculatus*. It is not present with *maculatus* in the low heather (6) along the western margin of Saltings Strip, nor indeed, except in the north, does it occur in any of the country between this and the stream (types (4), (5) and (7)). In the north there seem to be only two suitable areas and both are occupied: a short strip of tallish grass running from the north-east shore between two dunes, and the grassy banks of Northern Enclosure.

West of the stream *bicolor* is present on the drier grassy parts of Northern Enclosure, and here and there on the banks and in the coarse grass on either side of them. It was taken, though again less frequently than *maculatus*, along most of the habitable parts of the roadside (10). Between this and the stream, apart from two type (5) loci (Pl. I, phot. 1) near the road in the north, it was found in three places only:

(*a*) Within Plateau Enclosure (9), where it is plentiful and the predominant species (see p. 67).

(*b*) In a type (6) locus, low grasses and heather with some gorse bushes and birch trees, on the border of Central Marsh near where the stream leaves Little Sea; this isolated colony is surrounded on three sides by swamp and water and on the north by acres of unpopulated heather. The heather nearby has recently been extensively burnt, but the colony escaped.

(*c*) A small population some 200 yards west in the dryish tall grass margins round the point of Little Sea by Curlew Cottages; this little colony is again separated by some 300 yards of unpopulated heather from the nearest roadside population.

The species is represented, sporadically, along the length of the harbour shore (11), occupying, though thinly, more of this locus than any other species; and its colonies may be separated by as much as 200 yards of barren beach.

It is absent however from the short grass of Peter's Point and Southern Point and from Pleasant and Cluster Beetle B. It appears to require tall grassy herbage as a predominant element in the turf, but grass is not sufficient if it is as short as that of Southern Point. The open grass at Pleasant Southern is equally short, but the insects are to be found mainly in the longer grass round the riverside margins. P. II. plate 6.

The species has apparently reached and colonised every area within its range of tolerance.

M. maculosus Dewar, n.

The original host of this grasshopper was *C. viride* and its origin is usually the predominant species. This almost fully winged species (type A, B, C and many of type D, but scarcely any of the remaining series. In the landward edge of Peter Bridge (1) and (2) of P. III. plate 1 it is common enough to show the predominance of the dominants as they do. It was first encountered on the open heather ridges (type F and on the "seaside" of heather that was from the coastal depression, but usually it is confined to the river heather and grassy slope and in Peter Bridge. These insects in very heather gave the impression rather that they were either surrounded than part of a permanent population. It is doubtful also whether Pleasant Beetle either are the population of this species individuals were found in the heather north of Beetle Bridge Bay and similarly in places near the riverside. On Cluster Beetle it was taken with considerable and headquarters. It was present about 1 per cent. of the population on the grass at Pleasant Southern. P. II. part 1. Its absence in the grassy part of Northern Southern, though the dominants was taken in the heather part. All round Seaside Beetle Bay and surrounds the species was found on the grassy slopes of the north and on the low lying grass. It is absent from the short grass of Peter's Point, but is present on the grassy and the slopes were taken on the beach grass to about the west 20 yards northwards. Beyond this it was not found. In August 1901 it was noted on the short grass near the west end of Pleasant Point between 20th and 30 yards further south than in 1900 as such.

Generally speaking then, with the exception of the low beach grass the species avoids damp situations and does not appear to establish itself in regularly grassy fallows. It avoids pasture short vegetation and the presence of some short grass seems essential. Overall the turf is very coarse. From the taller grasses it is absent.

Neither the species nor the sex ratio seem to show a seasonal and yet numbers were not very great, as both were well-represented towards autumn. The most marked Pleasant and Cluster Beetle were caught very seldom and then as yet or are not to be encountered grass under consideration. It also as yet or are not to be encountered grass under consideration. It also as yet or are not to be encountered grass under consideration. The absence of specimens from Pleasant Beetle is explicable on the grounds that the suitable portion

in this area are all too wet for it; but why, having rounded Jerry's Point, it has failed to cross the 200 barren yards to the next possible locus, which is occupied not only by *bicolor* but by both Tetrigids, is not easily understood. It may be that the species has only a precarious hold on a locus as damp as the shore grass and that recolonisation is necessary after bad seasons; or that the population is made up only of adult stragglers. The northern part of the shore, where the species was present in 1931, is backed by populated heather and is also not far from the roadside.

The genus Acrydium.

The complete distributions of the two species of this genus are much more difficult to determine than those of the preceding species. Both species are quite small, they are mainly ground-living and their "protective" colouring is most effective. Their life cycle is such that at the time of our survey there was a high proportion of nymphs ranging through all stages of development and we did not feel competent to separate the two species in the field in their nymphal states. So in spite of the care exercised, we do not feel satisfied that recorded "absences" are quite in the same category as those for other species.

A. kiefferi (Text-fig. 4).

This species, like its two frequent associates *bicolor* and *maculatus*, has a wide range of tolerance. It shares with the latter a capacity to colonise heathery loci where *bicolor* is left behind, and with the former a tolerance of damp places which are not occupied by *maculatus*; but its exact ecological niche is not the same as that of either of them.

It was found in all locus types except the lakes (3), swamp (4) and the plateau heath (8); but curiously enough, except for one specimen found within Northern Enclosure, it does not extend further north than the top of Saltings Strip in the east and the corresponding level on the shore of Bramble Bush Bay in the west. It was found most frequently among low plants, but it may be that in such conditions the insect is more easily seen, for it is not confined to loci of this type. It was taken, for instance, in the comparatively dense and tall herbage of some of the marshy hollows (cf. Pl. I, phot. 1), and in the marshy border of One-acre Pool (5). It is all down the dunes and continues round Eastern Lake towards the border of Little Sea. Though not found where there is nothing but marram, it does appear to press further into the dunes than any other species, occasionally reaching the dips on the crest of First Ridge. Its distribution by the north-east coast is instructive. On the west side of Saltings Strip there is a wide, flat belt, not more than a foot or so above sea-level, lightly covered with low, recently burnt, heather; shorewards this gives way to open sand sparsely covered with fine grass. Both *kiefferi* and *maculatus* were present in the heather, but only the latter apparently has invaded the grass. On the eastern side of the strip the low dunes break off abruptly owing to coastal erosion; here *kiefferi* was found

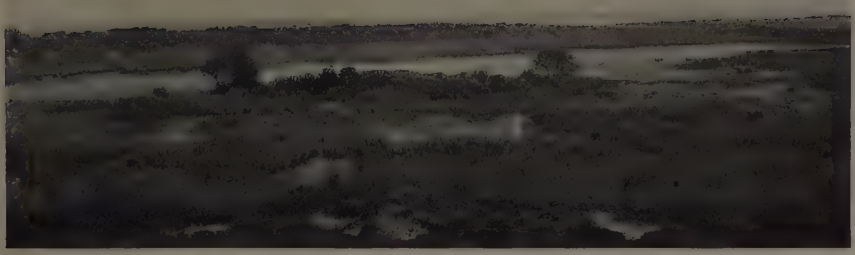


Photo. E. J. H. Edenborough, May, 1932

Phot. 5. View from a First Ridge dune, looking northwards along Saltings Strip over Eastern Lake and its island; in the middle distance on the right First Ridge (*Psamma*), in the centre Second Ridge (*Calluna*).

Photo. E. J. H. Edenborough, May, 1932

Phot. 6. The central tongue of Saltings Strip, looking south-west; scattered grasses and *Carex arenaria* in the foreground, then the denser saltings vegetation, and in the middle distance First Ridge dunes.

right up to the edge of the dunes while *maculatus* stops a little further inland. There is less growing vegetation (except marram) in this locus than is provided by the fine grass on the other side, but on the floors of the little dips there is a thin coating of dried vegetable detritus, which is absent from the grassy sand. It seems not improbable that *kiefferi* depends mainly for food on dead vegetable matter or the minute plants growing on it, while *maculatus* requires growing grass.

The species flourishes in the drier parts and margins of the Saltings Strip (2) (Pl. III, phot. 6). Between the strip and the stream it was found sporadically in low heather on the flatter parts and on the edges of Second Ridge, but not on the Ridge proper. In the country between the stream and the northern arm of Little Sea, except for a colony at the southern end (with *bicolor* and *maculatus*, p. 58, colony (*b*)), it is only very sparsely present. North of this it becomes more frequent, particularly around One-acre Pool from which it reaches eastwards as far as the sallow clumps on the borders of Central Marsh. It occupies the roadside (10) down to Plateau Enclosure, and the enclosure itself (9). (In August, 1932, this species and *bicolor* were recorded from the roadside well south of the southern end of Plateau Enclosure.) On the harbour shore its distribution is much the same as that of *subulatum*, except that it stretches some 300 yards further north, and that there is an isolated record from the extreme south.

This insect, therefore, will tolerate surface conditions ranging from wet to dry, though not standing water, and several distinct plant communities ranging from low to comparatively, but not uniformly, high herbage, and from sparse to dense plant population.

The northern limits may be set, partly at least, by the absence of obviously suitable loci, but this cannot be said of the plateau. The vegetation there is low and not dense, and much of the area is less damp than many places which the species occupies quite happily. Apart from the three shore colonies, Plateau Enclosure (Pl. II, phot. 4) and a part of the roadside, it was found nowhere on the Bagshot beds. Though recorded from the shore in the extreme south, it has apparently not crossed the 150 yards to join the other three species on the roadside south of Curlew Dyke. There must be something definitely unpleasant about the plateau area to make it uninhabitable to a species as accommodating as this. The presence of this grasshopper on the island in Eastern Lake suggests either that it was isolated there when the lake was formed, or that it reached the island after a very dry summer, for its wings are poorly developed. Swimming, however, is a possibility (Pl. III, phot. 5).

A. subulatum (Text-fig. 4).

It can hardly be said that the distribution of this species is geographically limited, as the two pairs of localities are separated by the width of the area, but it is definitely localised. In all loci the population was thin and markedly

inferior in numbers to that of its congener, without which this species was not found established. This association is not general, cf. Wicken Fen (Lucas (**2**)), and Lucas (**1**) says that *kiefferi* is usually found in drier places than *subulatum* which prefers marshy spots.

At the northern end of Saltings Strip the species was found here and there in the main strip and in the north-eastern tongue. In June, 1931, one specimen was taken in the evening by sweeping the tops of the rushes in the middle of the main strip, but at the time of our survey sweeping the rushes either in the day or in the evening produced none. It was found most freely along the edges, and among the low plants and short grass that grow in the open patches and along the rabbit paths. Southwards it may be present here and there down the strip, but adults were not again recorded until the central tongue, that runs out towards the shore through a gap in First Ridge, was reached. The taller vegetation in this tongue is thinner and the ground is drier; rushes and bog myrtle are present, but the ground is mostly covered with short grass; round the edges a fine grass is thinly scattered over the sand. Here the Tetrigid population is dense and *subulatum* reaches its maximum frequency (Pl. III, phot. 6).

Apart from this area, there are two scattered populations on the harbour shore:

(*a*) round Bramble Bush Bay to Jerry's Point, and

(*b*) after an apparent gap of 300 yards, along the shore southwards to about the middle of Dyke Bay.

The general conditions in these bays are not very unlike those of Saltings Strip. In April, 1931, one specimen was taken from a sandy patch near One-acre Pool, but none was seen there during the August survey. Throughout the rest of the area surveyed the species was seemingly absent.

This species does not follow *kiefferi* into the dunes, though the marginal area round the central tongue is dry and might almost be described as type (1), or into the heather, so it is absent from locus types (6), (7) and (8). Its absence from loci of types (3), (4) and (5) is no doubt due either to the presence of too much surface water or to the absence of the coating of low vegetation which it seems to like. Plateau Enclosure (9) and the roadside (10) are presumably too well drained.

It is an interesting fact that the four existing centres of population have only reached their present condition of development quite recently. The north-eastern and central tongues of the Saltings Strip were not in existence in 1900, though at that date other parts may have been suitable. Some saltings existed in Bramble Bush Bay in 1886, but the main development in both bays has apparently taken place since 1900. The species would thus seem to have no difficulty in spreading, and in the absence of further information its patchy distribution must be ascribed to its limited range of tolerance.

X. FACTORS LIMITING THE RANGE OF LOCI OCCUPIED BY DIFFERENT SPECIES.

The distributions given above do not suggest obvious associations, except for that of *dorsalis* and rushes, between any of the species and any particular plant. It is hoped that detailed comparisons will be possible later when the plant maps are available. For Acridid populations the presence of some not too dense grass appears to be a *sine qua non*, but even this does not seem essential to the Tetrigids. The presence of heather in any quantity is a useful indicator of the probable absence of *bicolor* and *subulatum*, and, so far as our information goes, *albomarginatus* and *viridulus*; but none of the remaining five species are limited to heathery areas. The quantity of soil surface moisture, and the height and density of the herbage, are obviously factors of some importance. These two factors are to some extent interdependent, but it is with the grosser degrees of wetness that we are mainly concerned.

The eleven locus types, arranged roughly in an order of decreasing wetness, give Table I. The order of the locus types within the four main groups is of necessity somewhat arbitrary; for instance, the conditions round the harbour shore saltings are drier than many marshy spots, but are very similar to parts of Saltings Strip; other parts of the strip can be more evenly wet than any normal type (5) locus.

Table I. *Classification of locus types roughly in order of decreasing wetness.*

	Soil surface	Locus type	Vegetation
Standing water present	Completely covered	Lakes (3)	Not dense, moderately tall
	Partially covered	Swamp (4)	Very dense and tall
Variably damp	Each ranging from wet to merely moist surface	Saltings (2)	Not dense, moderately tall, patches quite short
		Marshy spots (5)	Not dense, short to moderately tall
		Harbour shore (11)	Not dense to sparse, moderately tall to quite short
		Plateau (8)	Not dense, usually short
Bordering	Dry, but usually with damper ground near	Bordering heather (6)	Not covering soil, short
		Roadside (10)	Not dense to sparse, mostly short
Dry	Flat	Plateau Enclosure (9)	Covering soil and short, or dense and moderately tall
	Sloping	Dunes (1)	Except for marram tufts, sparse and short
		Heather ridges (7)	Mostly dense, and moderately tall

If the commoner grasshoppers are arranged in the order of their increasing tolerance of drier conditions, and their recorded "presences" plotted against the classified locus types (Table II), the reasonably continuous distribution of each species gives a fair idea of the importance of wetness as a limiting factor.

Table II. *The distribution of the nine grasshopper species in relation to the different locus types.*

		C. dorsalis	*A. subulatum*	*M. brachyptera*	*C. parallelus*	*C. bicolor*	*A. kiefferi*	*M. maculatus*	*C. albomarginatus*	*O. viridulus*	Totals
Standing water	Lakes (3)	+	.	.	.	.	.	.	.	.	1
	Swamp (4)	+	.	.	.	.	.	.	.	.	1
Variably damp	Saltings (2)	+	+	.	.	+	+	.	+	.	5
	Marshy spots (5)	+	+	+	+	+	+	+	+	+	9
	Harbour shore (11)	+	+	+	+	+	+	+	.	.	7
Bordering	Bordering heather (6)	.	?	+	+	+	+	+	.	.	5
	Roadside (10)	.	.	+	+	+	+	+	.	.	5
Dry	Plateau Enclosure (9)	.	.	.	+	+	+	+	.	.	4
	Dunes (1)	.	.	.	.	+	+	+	.	.	3
	Heather ridges (7)	.	.	?	.	.	?	?	.	.	
	Totals	5	3	4	5	7	7	6	2	1	
Special type	Plateau heath (8)	.	.	+	+	.	.	+	.	.	3
Number of squares occupied		40	10	45	42	48	53	55	5	2	

The plateau heath (8) has been shown separately because its geological distinctness from the rest of the area introduces a complication with which we are not here concerned. Disregarding this difference, it is really a mixture of locus types (5) and (6) with its sloping edges approximating to type (7), and the tolerance range of the species that can stand its special conditions is already adequately shown under these types.

The two species, *albomarginatus* and *viridulus*, have been placed at the end of the table out of their proper order because they are too "rare" in this area for any picture of their true range to be obtained.

Only one species, *dorsalis*, occupies areas in which there is permanently standing water, whereas all nine are found in variably damp loci. The absence of *brachyptera* from Saltings Strip may be an ecological absence (p. 57), but, if so, it is more probably due to unsuitable vegetation or other causes rather than to degree of wetness. The northern part of the strip is certainly not too wet for *parallelus* and it is possible that this absence may be due to geographical causes (p. 53). On the other hand, the absence of *maculatus* is clearly significant, as it is found all round the strip on both sides, and though there may be other contributory causes, wetness is surely one.

In the bordering types only five species are recorded. *Dorsalis* is excluded owing to its association with rushes; but *subulatum* may wander on to these types (e.g. by One-acre Pool), though it seems doubtful if it would establish itself there. Probably *albomarginatus* is a true absentee, but *viridulus* can occupy really well-drained slopes (e.g. Corfe Castle), so that the unsuitability, if real, of these loci would depend more on the sparseness and shortness of their vegetation.

Passing into the dry group the number of species is reduced to four by the loss of *brachyptera*. The difference between the three types of locus in this group lies mainly in the vegetation. In our experience the areas of deep and

almost pure *Calluna* have no established population though *maculatus*, *kiefferi* and *brachyptera* may be picked up. The absence of *parallelus* from the dunes is possibly significant, and if so the reasons are probably similar to those given above for *viridulus*.

The classification of the loci in terms of vegetation density and height (Table III) cuts right across the main locus types, and with our present information it must be rough; but it gives some idea of the different degrees of tolerance and the importance of these factors in limiting the range of habitat.

Table III. *The distribution of the nine grasshopper species in relation to vegetation density and height.*

		C. dorsalis	*C. albomarginatus*	*C. parallelus*	*M. brachyptera*	*C. bicolor*	*M. maculatus*	*A. kiefferi*	*A. subulatum*	*O. viridulus*	Totals
Dense	Very tall	.	.	.	.	.	.	.	.	.	0
	Tall	+	.	.	.	.	.	.	.	.	1
Looser	Uniform; moderately tall	+	+	+	+	+	.	.	.	+	6
	Not uniform; moderately tall and short	+	+	+	+	+	+	+	+	.	8
	Uniform; short	.	.	+	+	+	+	+	+	.	6
Sparse	Not uniform; moderately tall and short	.	.	.	.	+	+	+	+	.	4
	Uniform; short	.	.	.	.	+	+	+	+	.	4
	Totals	3	2	3	3	5	4	4	4	1	
Number of squares occupied		40	5	42	45	48	55	53	10	2	

XI. The grasshopper communities.

The limiting factors considered in Tables II and III form a useful basis upon which to classify the different communities found in this area. Where several species are enumerated, one or more may be absent in any particular locus; our information is not sufficient to allow us to say whether such absences are significant or not. For reasons already given (p. 45), we did not in fact find more than six species in one locus.

Vegetation uniformly and moderately tall (*maculatus* and the two Tetrigids which are predominantly ground species are absent from this group):

(*a*) In dense marshes with rushes: *dorsalis* alone.

(*b*) In damp patches of bog myrtle, grasses, rushes and some heather, as in the north of Central Marsh: *dorsalis*, *brachyptera* (a frequent association: see Text-fig. 3).

(*c*) In similar but more grassy spots: *dorsalis*, *brachyptera*, *parallelus*, *bicolor*, *viridulus*.

(*d*) In saltings type; rushes predominant: *dorsalis* alone; *dorsalis*, *bicolor*; *albomarginatus* alone; *dorsalis*, *albomarginatus*.

(*e*) Grasses predominant: *albomarginatus*, *bicolor*; or with *brachyptera* added.

(At Lilliput: *albomarginatus*, *parallelus*.)

Vegetation not uniform, some low some taller, with or without bare patches (in this group, naturally, all the species do not occupy exactly the same "niche"):

(*f*) Marshy or damp spots and harbour shore saltings, heather usually absent: *dorsalis, brachyptera* (absent from the rushes of the saltings), *maculatus, parallelus, bicolor, kiefferi, subulatum* (or some combination of these).

(*g*) Slightly drier spots, shorter vegetation, some heather: *brachyptera, maculatus, parallelus, kiefferi*; or *brachyptera, parallelus*; or *parallelus* alone.

(*h*) Similar, but grassy (Northern Enclosure): *albomarginatus, bicolor*, possibly *maculatus, kiefferi.*

(*i*) Plateau Enclosure: *bicolor, parallelus, maculatus, kiefferi.*

(*j*) Dunes: *maculatus, kiefferi, bicolor* (all down the landward side of First Ridge: see Text-fig. 4).

(*k*) Roadside, grassy: *maculatus, bicolor, parallelus, kiefferi* (sometimes *brachyptera* in the ditches).

Vegetation uniformly low (*dorsalis* and *albomarginatus* are absent from this group and in this area *viridulus* also):

(*l*) Marshy: *brachyptera, parallelus*; or either alone.

(*m*) Slightly drier, heathery: *brachyptera, maculatus, parallelus* (Curlew Heath).

(*n*) Shore grass: *bicolor, maculatus, kiefferi*, sometimes *subulatum.*

(*o*) Saltings margin: *maculatus, kiefferi*, sometimes *subulatum.*

(*p*) Bordering heathery types: *maculatus, kiefferi*, sometimes *brachyptera.*

(*q*) More grassy bordering types: *bicolor, parallelus, maculatus, kiefferi.*

(*r*) Dune margins: *maculatus, kiefferi, bicolor.*

(*Note.* In (*h*), (*i*), (*j*) and (*r*) the species are arranged in the order o numerical predominance. In the other cases, there are either too many sub types or insufficient information to attempt any such order.)

Recent physiographical changes must have had considerable effects upo the distribution of these various communities. To-day, the three most fre quently recorded species are the three members of the typical "dry" com munity, *maculatus, kiefferi* and *bicolor* (see p. 44); the next most frequen species are the three members of the "damp" group, *brachyptera, parallelu* and *dorsalis*, recorded for about ten squares fewer than the preceding com munity. The development of the marshes during the last thirty years (se Text-fig. 2) must have largely increased the area available for the *brachyptera dorsalis* community and have allowed *parallelus* to spread beyond the Bagshc beds. It seems very probable that the advance has been made at the expens of the "dry" community, for the grasses and short heather that apparentl used to cover the flatter part of the central area should have provided suitable locus for it. The now completely isolated colony of this triple com munity at the southern tip of the central area (colony (*b*), p. 58) may we

be the last remnant of a much more widely spread population. The present "marginal" distribution of heather has no doubt been brought about by the slow encroachment of heather over grasses as the land has been built up eastwards. The development of the Salmas Strip between 1930 and 1940 put a large new area at the disposal of *borealis* and the Terrapins. On the other hand if the barren swamp continues to encroach on the less developed parts of Central Marsh the area available to *borealis* and *insulaepyrrhi* will suffer restriction (see Text-fig. 3).

XII. Population intensity.

The words "population intensity" can be used in at least three senses. They may refer to the absolute density of a localised population, i.e. to the number of grasshoppers per square yard irrespective of species; to the relative frequency of the different species composing such a population; or to denote the degree to which a species occupies the available suitable land.

In any season the absolute density of a localised population obviously depends upon two, and probably upon three, interacting factors: i) the closeness with which the locus approaches optimum conditions, ii) the meteorological conditions of the particular season, and iii) the possible presence of some periodic rise and fall in population numbers. We know of no attempt to determine the existence or absence of population cycles in these particular species (though other Acrididae, e.g. *Locusta migratoria*, show periodicity), but the possible effects of this phenomenon must not be overlooked. Owing perhaps to a poor season and to shortness of time, we were unable to make comparisons between optimum loci and those on the margin of tolerance, or to make accurate counts over measured areas; but the following two samples made from areas of approximately the same size, between two and three acres, and in different locus types, give a very rough idea of the absolute densities and the relative frequencies in the more thickly populated parts in 1951.

The first sample was taken from the marshy sides (5) of One-acre Pool, the east and west sides being kept separate, the second from the grassy part of Plateau Enclosure (9):

	One-acre Pool		Plateau Enclosure
	East side	West side	
insulaepyrrhi	4	1	—
borealis	28	30	—
parallelus	7	23	8
albicornis	—	1	69
brachyptera	1	24	4
apicalis	2	4	1
Total	42	84	82

The two sides of the pool were kept separate because on the west side the lake margin (5) passes without any definite barrier into the roadside (10), and it consequence it was expected that the two samples might show a

significant difference. When compared with each other by the χ^2 test, the value of P is 0·00416, or the chances against the two samples being drawn from the same population are about 240 to 1. The difference is brought about by the far higher proportion of *dorsalis*, the lower proportion of *maculatus* and the absence of *bicolor* on the eastern side, the two latter being predominantly roadside species.

The differences between the two lakeside samples as compared with the Enclosure sample are so obvious as to need no comment. Taking into account the size of the respective areas, the three samples do not reveal any striking differences in the densities of the total grasshopper populations. No populations on South Haven Peninsula showed anything like the density of a population, sampled during the same fortnight, from the steep grassy banks below Corfe Castle. Here a sample of 163 was easily taken from an area certainly less than one acre in extent containing:

bicolor	parallelus	viridulus
106	55	2

In 1930 the Lilliput population of *albomarginatus* yielded about 150 specimens when only a few square yards were swept. (The nymphal population seen earlier in the summer, both in 1931 and 1932, seemed to foreshadow a greater density in the August population of adults than was actually found. It is difficult to imagine that the same marked difference between nymphal and adult population density could have been present in the Lilliput population. The presence of the sand lizard (*Lacerta agilis*) on South Haven Peninsula may be one of the factors causing this population reduction.)

In a species with an annual life cycle, the degree of occupation, that is, the proportion that the number of spots actually occupied bears to the total number that appear to fall within the animal's range of tolerance, must obviously differ considerably in different years, and in comparison with longer-lived organisms must be far more sensitive to the effects of the three factors mentioned above. In a bad season, whether due to poor weather conditions, or to its falling in the trough of some periodic system, or to both causes combined, it is more than probable that loci near the margin of tolerance may completely lose the population that they are capable of sustaining, and do in fact sustain, under better conditions. At such a time apparently suitable loci, normally populated, may be recorded as barren gaps in the distributional continuity. It may reasonably be supposed that in those species that have a fairly wide tolerance, as most of these species have, the marginal area over which contraction and expansion can take place is likely to be wider than in those species where the degree of tolerance is very limited.

XIII. Summary.

The distributions of the nine species of grasshoppers inhabiting South Haven Peninsula have been mapped, and the different types of plant communities roughly classified. The effects of recent physiographical changes upon these distributions have been discussed.

The range of tolerance of each species, as exhibited by its distribution in this area, has been roughly determined in regard to degree of wetness, vegetation height and density, and type of plant community. It has been shown that these are among the factors that determine the distribution of grasshopper species. The effects of geological differences within the area have been considered.

The percentage of occupation by the grasshopper population as a whole has been roughly measured.

The different grasshopper communities found have been considered in relation to the different types of locus, and some figures of population samples have been given.

We are much indebted to Mr B. P. Uvarov, Mr R. D'O. Good and Prof. E. J. Salisbury for help and advice in the preparation of this paper; to Dr P. A. Buxton for help in the field during August, 1932; and to Mr E. J. H. Edenborough for taking the photographs.

REFERENCES.

(1) **Lucas, W. J.** (**1920**). "A monograph of the British Orthoptera." London (Ray Society Monographs).

(2) **Lucas, W. J.** (**1925**). "The Natural History of Wicken Fen" (edited by **J. Stanley Gardiner**), Part 2, 69–75.

(3) **Uvarov, B. P.** (**1930**). "The Orthoptera of the British Isles." Société de Biogéographie, III. Contribution à l'étude du peuplement des îles britanniques, pp. 57–65.

THE CROP OF CEDAR NUTS, INVASIONS INTO EUROPE OF THE SIBERIAN NUTCRACKER (*NUCIFRAGA CARYOCATACTES MACRORHYNCHUS* BREHM) AND FLUCTUATIONS IN NUMBERS OF THE SQUIRREL (*SCIURUS VULGARIS* L.)

By A. N. FORMOSOV.

Laboratory of Zoology, Moscow University.

(*With three Figures in the Text.*)

I. Introduction.

The present article is a preliminary communication of one of the author's works connected with an extensive cycle of researches organised with the object of studying periodic fluctuations in the numbers of fur animals and game birds in the territory of the U.S.S.R. Fluctuations in numbers are very widespread among the tundra, taiga and steppe animals of Northern Asia, and therefore investigations in this domain are exceedingly necessary. The author is most grateful to the editor of *The Journal of Animal Ecology* for giving him the opportunity of publishing his article in the pages of this journal.

II. The cedar (*Pinus cembra sibirica* Mayer) as a food plant.

The nuts of the Siberian cedar constitute one of the most important sources of food for a great many animals of the taiga. Forest mice, numerous species of voles, chipmunks and squirrels among Rodents, the sable and the brown bear among Carnivora, boars and deer among the Ungulates, and many species of birds have constantly recourse to this food.

Possessing highly nutritive qualities, like the majority of the seeds of Coniferae, the endosperm of the cedar nut is distinguished advantageously by its large size, so that even such a huge animal as the brown bear can, in a comparatively very short time, appease his hunger with cedar nuts. The following table, made from the data of Morosov (**10**), Solskij (**21**), and the author, shows the difference between the weights of the seeds (deprived of their wings) belonging to the most widely distributed Coniferae of the taiga, and that of the cedar nuts:

Table I. *Weight in grammes of* 100 *seeds of various conifers deprived of their wings, and of* 100 *cedar nuts.*

Fir	0·28–0·70
Pine	0·34–1·00
Siberian spruce	0·63–0·80
Siberian larch	0·67–0·98
Siberian cedar	30–35

On every cedar tree there are from 30 to 300 or more cedar cones (Ivanov (6)), on every fir, pine or larch, in conditions favourable for fruit bearing, from several hundred to a thousand or more cones. But as a total the crop of small conifer seeds (as calculated by Russian foresters) is rarely above 1–10 kg. on 1 hectare, whilst one can gather up to 250,000–300,000 kg. of cedar nuts from a hectare (Grocholskaya (5), data for middle Siberia). Finally, this is what determines the exclusive rôle of the Siberian cedar as the most important of the food plants of the taiga; although within the limits of the area of different species of Coniferae, it only dominates (taking the number of trunks) less than 10 per cent. of the entire forest surface, and in other places it is only found as an admixture in forests of fir, spruce and larch.

III. The importance of cedar nuts in the nourishment and life of the squirrel (*Sciurus vulgaris*).

As regards the squirrel (*Sciurus vulgaris*), represented within the limits of the cedar area by several sub-species, we do not at present possess sufficiently extensive data on the analysis of the squirrel's stomach contents to judge accurately what is the importance of the cedar nut in the nourishment of the squirrel. There are, however, very numerous direct observations, indicating a rather close dependence of this rodent upon the cedar everywhere within the limits of the latter's area of distribution. If we turn to the publications of recent years, we shall see that Shuchov (15) for the Tarsk district, Troitzkij (24) for the Tahudino-Angara district, Naumov (11) for the Turuchansk region, Pogudin (13) for the Kirensk district, Zverev (26) for the province of Minusinsk and Chakasia, Soloviev (20), and the Kozhantshikovs (9) for the mountain country of Sajan, Petrie (12) for the hunting district of Tutursk, and a multitude of other authors who have previously written about the Siberian hunting trade, notice the pre-eminent and exclusive importance of cedar-tree groupings and of the crop of cedar nuts in the life of the squirrel.

The preference squirrels show for cedar forests when settling down, their migration to cedar regions[1] when there is a crop of cones, constant occurrence of squirrels on trees of this species during feeding time, the multitude of cedar cones injured in a characteristic manner by squirrels, the existence of winter stores of cedar nuts made by this little animal, the dependence of the time when the fur-shedding begins and of the course it takes upon the crop of cedar nuts, as well as other facts frequently noticed by observers, all show with sufficient clearness that this species of forest tree plays a considerable part in the ecology of the squirrel.

[1] The Siberian cedar is distributed from the middle course of the Pechora across Middle and Northern Ural all over Siberia as far as Jakutia and the region above lake Baikal.

IV. The periodicity of the cedar-nut crops.

Like other species of Coniferae the cedar does not give a good crop every year: on the contrary a year of abundant seed-bearing is followed by several years with a smaller crop, or no crop at all. For Verchoturje (Ural), Walewsky (25) gives a recurrence of the large crops every 2–3 years, Sonine (22), for Tscherdyn, every third year (though with an insufficient constancy), Kaplan, for Middle Siberia, every fourth year, Kokoulin (8), the same for the districts of Vercholensk and Balagansk (basin of the Lena). Judanov (7), for the Narym country (to the north-west of Tomsk), with its less favourable conditions, describes the periodicity of these crops as follows: "According to the observations of traders, there is almost always an order of this sort in the alternation of nut crops: there are four years running of good crop seasons, with a maximum yield the second year; then there is an interval of 8–10 years with bad crops when scarcely any one gathers nuts." Lastly, Ivanov (6) gives the following data for the district of Irkutsk: "In the northern and eastern part of this district, there have been three good crops in the course of the last 10 years, five middling and two bad ones; in the western part, the crop was good in 1927, middling in 1929, in two years there were no nuts at all, and in the others the crop was below the average."

In spite of the somewhat variegated picture presented by the fruitfulness of the cedar in different years and in different regions, it is nevertheless comparatively easy to perceive from the fragmentary data on the amount of nuts conveyed by rail, and from the fluctuations of the prices, that sometimes the bad crops can extend simultaneously over an immense territory. This is natural, for the fruitfulness of the cedar, besides depending upon internal physiological causes, is assuredly controlled by certain climatic factors, not closely studied as yet, which perhaps are vital in the period of flowering or in the early stages of ripening of the cones. The deviations in the incidence of climatic factors from the mean of a long series of years (to which, in certain biological phenomena, the cedar has adapted itself), occur over immense spaces of the almost completely flat plains of the whole western and middle parts of Siberia.

V. Fluctuations in the number of squirrels.

It is evident that such sharp fluctuations in the quantity of the most important food, over such an extensive stretch of territory, must react very sharply on the biology of immense populations of animals ecologically closely connected with the cedar.

We may assume that in the conditions of a very bad crop of cedar nuts, the squirrel population, within the limits of the cedar's distribution, must suffer severely. One is greatly tempted, on the grounds of some indications given by trappers, to connect the well-known fluctuations in the number of

squirrels, formerly appears in the amount of fur goods obtained, with the periodicity of fruit-bearing in the cedar. This does partly suggest itself also because the periods of a rise in the number of squirrels in many places on the fourth year after three years, on the fifth after four, approach rather closely those of the good crop years of the cedar.

The years when a good trapper takes as many as 200–300 or more squirrels are usually followed by seasons when, with a much greater expenditure of effort, a hunter collects 50–150 or even fewer skins. The success of the hunt depends chiefly upon the actual quantity of squirrels and in a lesser degree upon all sorts of trapping factors and economic causes. Thus the number of squirrels taken in separate villages will furnish a good indication of the quantity of squirrels in neighbouring forest areas. In studying such complex phenomena as the periodical fluctuations in numbers of forest animals it is absolutely necessary to wait for one's conclusions to crystallize, and as far as possible, homogeneous statistical material over many years.

As regards the squirrel, whose skins year by year were brought to numbers of thousands from definite regions to particular fairs under the Tsarist Russian Empire, we possess sufficiently trustworthy and abundant if not altogether homogeneous material. Since these fluctuations in numbers of the squirrel in different parts of immense forest territories do not coincide entirely either as to time or to place, the fairs at the skins brought to the fairs give a rather distorted and exaggerated picture of the fluctuations in the squirrel population. Likewise the mass migrations of squirrels, a phenomenon of wide occurrence in the taiga, very strongly affect the number of squirrels in limited regions but cannot have a perceptible influence on the volume of the fur trade which reflects an "harvest of skins" on a territory of many hundreds of thousands of square kilometres. It was just such a province that supplied the fine fur from the basin of the river Pechora and the western slopes of the Ural to the Yenisei-Lena watershed, "fur of Siberia" proving a rôle subordinate to the former, and the Eastern fur from the watershed above mentioned to the west to the basin of the river Amgun and the mountain passes to the Pacific sea-coast in the east.

Up to very recent years the squirrel fur trade in Siberia was very little developed and existed on rather narrow territories. The commerce of such a town itself usually limited to within a radius of 30–50 kilometres from the village; it was more frequent than the fur trade, and as our investigations left us not much material, because as we have mentioned the squirrel skins prepared for trade. To overcome the difficulties rose mainly in the result of the fluctuations of the cedar nut crop in Siberia the author had recourse to a certain "re-way" utilizing the behaviour of the Siberian nutcracker. Nucifraga caryocatactes sibirica Brehm. as an indicator of the state of the cedar nut crop.

VI. The Siberian fine-billed nutcracker and its invasions into Eastern and Western Europe.

There is no doubt that the evolution of the nutcracker, belonging to the species *Nucifraga caryocatactes*, went on in the past side by side with that of the cedar, depending directly upon it, and in its turn controlling the actual dissemination of this conifer. The distribution of the cedar, as the recent work of botanists has shown (in Russia, Pohle(**14**) and Gorodkov(**4**)), proceeds exclusively by the nutcrackers carrying the cedar nuts about and burying them in the ground, amassing in this way a store for the winter. The nuts falling to the ground with the cone germinate very rarely. In the bill of the nutcracker there is a very curious apparatus which breaks the nuts. It consists of a semicircular cavity on the palatal side of the upper half of the bill (in its basal third), and of a hard elongated rib, correspondingly situated on the lower part of the bill. This is not all; in addition, the bill of the European nutcracker, whose distribution area is historically connected with the province occupied by the European cedar, bearing hard-shelled nuts, is massive and thick, whilst the bill of the Siberian nutcracker, confined somewhat rigorously in its distribution to the area of the Siberian cedar, is comparatively thin and weak, as is the shell of the Siberian cedar nut.

In the food of the nutcracker the nuts of *Pinus cembra sibirica* play an essential rôle. From July, having finished nesting, this bird begins to wander, seeking out clumps of fruitful cedar trees. Having found them it passes the autumn there, destroying an enormous quantity of nuts and storing them for winter in fissures of branches, holes among the roots of trees near the stems, under moss, and in rock crevices. In the years when food is abundant, the nutcrackers remain for the winter in their native forests and easily survive frosts, even the severe frosts of Jakutia. During the whole winter they feed upon their stores[1], digging them out easily from under the snow, and, even in the beginning of summer and in spring, when the next crop is as yet far away in the future, the stomach of this bird is stuffed with the kernels of the nuts hidden by the birds almost a year ago and found again.

We have said enough to show the close connection existing between *Nucifraga caryocatactes* and the cedar species in general, and between the Siberian cedar especially and the Siberian race of this bird, distributed to the east from the middle Petchora across the whole of Siberia.

The ornithologists who have worked in Siberia have noted many times that the numbers of the nutcrackers observed in their nesting places are very variable: some years there are a great many birds, whilst in others they are exceedingly rare, even in depths of the taiga where human beings have rarely ventured. As far back as 1837, Gebler(**3**) remarked this for the moun-

[1] The cedar cones fall off the branches whole in August–September, full of nuts, whilst in the majority of other conifers the cones remain hanging down all winter and lose their seeds only towards spring.

tainous Altaj, and Sushkin (**23**) for the taiga of the Sajan mountain ridge. These fluctuations in the numbers depend principally, as we shall see later, upon the preceding state of the cedar nut crops, and in connection with it, upon the hungry or well-fed state of the birds, upon their desertion of the usual winter quarters, and the great number of losses during migration. It is interesting to note that their connection with the cedar unites the squirrel and the nutcracker into a closely-knit ecological group. This is how the Tungus, the best trapper folk of Siberia, spoke about it to Petrie (**12**): "The nutcracker and the squirrel together live. When the nutcracker will come, the squirrel too will come [will be plentiful]. No nutcracker come, no squirrel, we always so observe."

Already for more than two centuries the observers of Western Europe have known about the periodically repeated invasions of this bird. The nutcrackers appeared sometimes in enormous numbers, usually in autumn, wintered in Western Europe (even as far as England), and remained sometimes in an insignificant number for nesting; but the greater mass of them perished on the journey and in places where they wintered, and as a rule did not return to their native land at all. No one has ever seen them on a homeward flight.

Owing to the comparatively large size, the curious mournful colouring and the unusual trustfulness of the birds coming from the scantily populated forests of the Ural and Siberia, the appearance of their flights always struck the eye, and was easy to trace not only in the west, but also in Russia, where there were fewer observers. Already as far back as the beginning of the eighteenth century, these invasions were regarded as "signs," foreshadowing wars, famine or pestilence, and brought terror to the hearts of the superstitious village population of the west. Later, when the native country of this bird had become known, these migrations were considered (also erroneously) as forerunners of rigorous winters, and continued to frighten the populations of the Ukraine, Poland and Germany.

There are very weighty proofs that the nutcrackers leave the regions where they regularly winter in the years with a normal crop of cedar nuts and migrate exclusively when there is an insufficiency of food, due to the absence of the crop of cedar nuts over a vast region (Slovtzov, Blasius, Gorodkov and others). Let us give only one example: in 1885 an immense number of nutcrackers flew over European Russia and invaded the forests of Western Europe. This migration was caused by a thoroughly bad crop of cedar nuts in 1884 and 1885 over the whole extent of the western half of Siberia. In the town of Tjumen the price of a poud (16 kg.) of nuts was 5 roubles, and in 1886 (a plentiful crop) it was 2 roubles (Slovtzov (**17**, **18**, **19**)).

Considering the observations quoted above, it is even difficult to suppose that there can be any other explanation. We have an analogous picture with the crossbill *Loxia curvirostra* L., also a stenophagous bird, when the crops of the fir-cones are bad.

VII. The invasions of nutcrackers in Europe and fluctuations in the number of squirrels in Siberia.

Having summarised, after studying a considerable literature, the data on the invasions of the nutcracker in Europe (without any pretension to an exhaustive completeness, as our own material shows sufficiently for our purpose the years of mass invasions over great distances), we will compare the dates thus obtained with the curves indicating the fluctuations in the numbers of squirrel skins brought to the fairs of Irbit and Jakutsk.

The furs concentrated here were obtained chiefly within the limits of the Siberian cedar's area, and at the same time from the typical trapping districts where the intensity of squirrel trapping is pretty constant; for, as has been

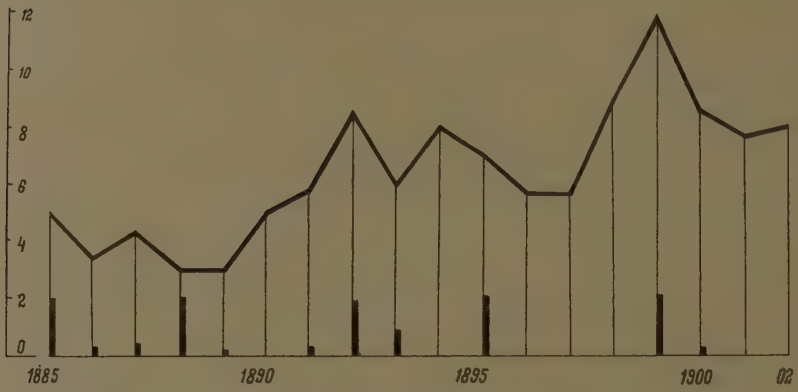


Fig. 1. Squirrel skins (in hundreds of thousands) brought to the Jakutsk fair from 1885 to 1902 and invasions of nutcrackers.

already said, the returns of the fur trading always held a conspicuous place in the budget of the population in those places.

In this manner the statistical data on these fairs, in spite of their being far from perfect, constitute the only material which can throw light on the numerical dynamics of the squirrel population, in so far as the latter are inevitably reflected in the relative success of the trade of squirrel skins. Both fairs are held at suitable times, at the end of the trapping seasons, i.e. the second half of winter and even partly in summer; therefore the data on the commercial dealings with the squirrel, represented by the transactions of the fair, giving the date of a certain year, must be referred to the trading season begun in the autumn of the preceding year.

The invasions of the nutcracker into the territory of Eastern Europe are usually noticed already in the autumn in which the birds leave their usual dwelling places. For South-western Ukraine and Western Europe they are

often dated from the first winter months of the following year, as the mass of the emigrating birds reach Germany and France only in January–February. In those cases when the nutcracker appeared in Western Europe the observations on the flight made in Eastern Europe are not mentioned.

Therefore the records of fluctuations in the number of squirrels are one year ahead, and this will characterise likewise some of the West European dates of the nutcrackers' invasions, if we endeavour by means of them to fix dates of the bad nut crops.

Table II gives this information in its unaltered form. The year-lag pointed out has not been eliminated in the graphs, in order to avoid confusion.

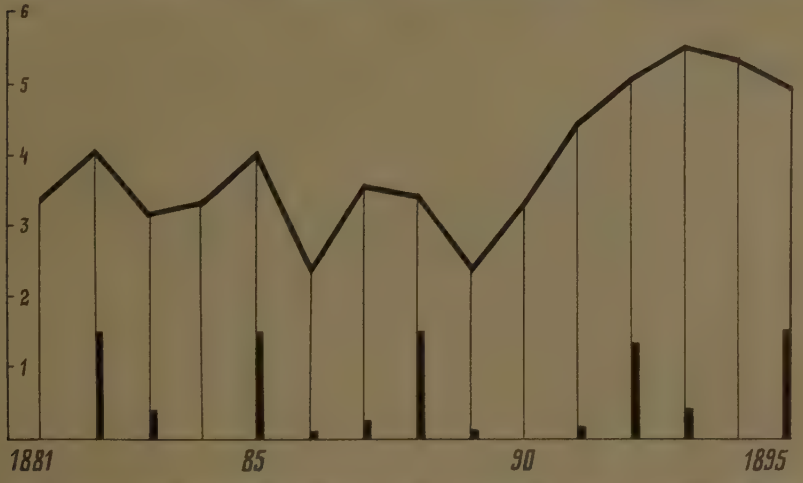


Fig. 2. Squirrel skins (in millions) brought to the Irbit fair from 1881 to 1895 and invasions of nutcrackers. The years 1892 to 1894 were years of bad corn harvest and famine; the population sold the furs in store and trapped intensely to increase its resources. This explains the unusual aspect of the curve giving the quantity of squirrel skins brought to the fair.

In reading either the one or the other, the need of such a correction must be taken into account.

On our graphs the years of the nutcracker invasions are represented by columns, whose height corresponds to the greater or less distance travelled by flocks of these birds westward and to the south-west. The following regular coincidences attract attention: the years with a decrease in the number of squirrels in the taiga coincide very constantly and exactly with the years when great quantities of nutcrackers appear in the south-west of the U.S.S.R., and in Western Europe. Especially large invasions of nutcrackers take place a year after a great arrival of squirrel skins at the fairs, i.e. after the years with an increased number of squirrels in the taiga (on the graphs they coincide, which is due to the peculiarities of the dating, see above). This regularity

Table II.

Date of invasion of the nutcracker in Europe		Years with a decrease of squirrel skins brought to the fairs ("Bad squirrel harvest")
1753 1754 1760 1793 1802	Western Europe	Data lacking as to the quantity of furs brought to the fairs
1812	Ukraine	
1814 1825	Western Europe	
1826	Ukraine	
1836 1844	Western Europe	
1846	Government of Voronezh	—
1847	Ukraine	—
1850	Ukraine	—
1851	Ukraine	1851–55 Fair of Jakutsk
1856 1857	Western Europe	— 1857 Fair of Jakutsk
1860–61	Lower Ural region Northern Caspic region	1859 Fair of Jakutsk
1864 1877 1878	Western Europe Government of Samara Eastern region near sea of Azof	From 1859 to 1885 data lacking on the squirrel at the Jakutsk fair
1882	Moscow province	1881 Fair of Irbit
1883	Western Europe	1883 Fair of Irbit 1884 Fair of Irbit
1885	Western Europe	1886 Fairs of Jakutsk and Irbit
1887 1888	Western Europe	1888 Fair of Jakutsk 1889 Fairs of Jakutsk and Irbit
1892	Moscow province, Ukraine	—
1893	Ukraine	1893 Fair of Jakutsk
1895 1896 1899	Western Europe	— 1896 Fair of Jakutsk 1897
1900	Bielorussia (White Russia)	1900 Fair of Jakutsk 1901
1903	Government of Samara	(From 1902 to 1913 data lacking on the squirrel at the Jakutsk fair)
1905	Government of Samara	1905–6 Fair of Irbit
1907	Western Europe	—
1908	Moscow province	1908 Irbit fair
1909	River Syr-Daria. Middle Asia, Podolia	—
1910	Nizhni-Novgorod region	—
1911	Western Europe	1912 Fair of Irbit
1913	Western Europe	1913 Fairs of Jakutsk and Irbit
1915	Lower Ural, Nizhni-Novgorod region	—
1917	Lower Ural, Nizhni-Novgorod region	
1921 1922	Kostroma	—
1923 1924	Ukraine	—
1927	Southern Ural, Western Russia	—
1928	Southern Ural	—
1929	Ukraine	—
1931	Southern Ural	—

proves the rapid response to bad cedar crops of the species connected with the cedar: at the same time the number of squirrels decreases visibly, the

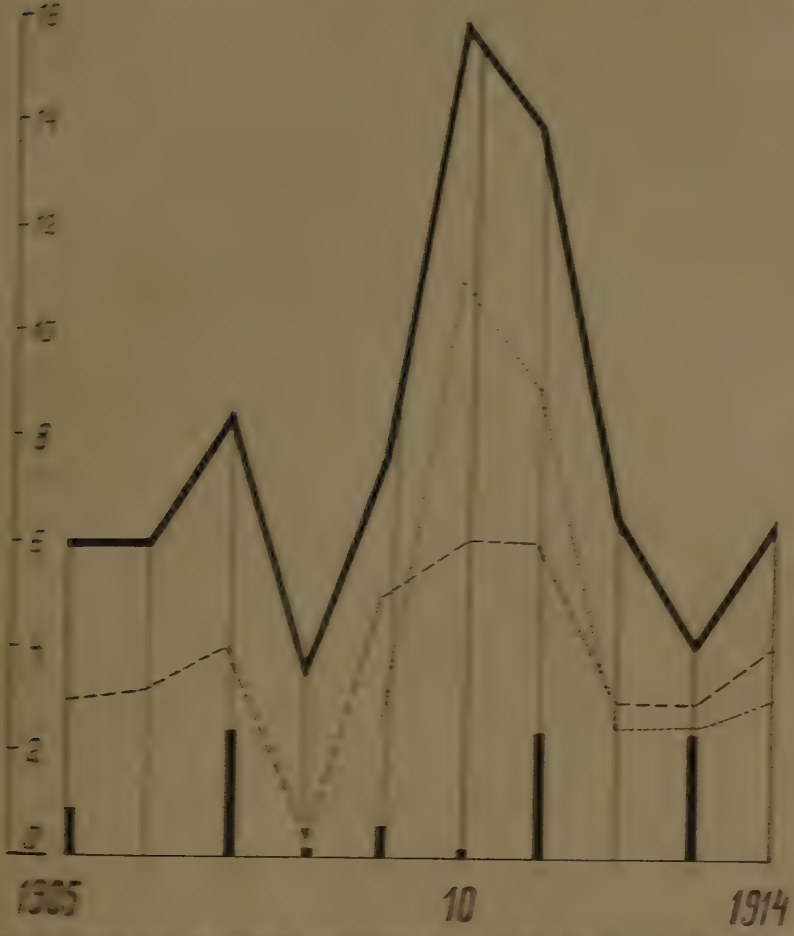


Fig. 1. Squirrel skins in hundreds of thousands brought to the Irbit fair from 1905 to 1914 and curvature of numbers. Thick line: squirrel skins from the river Pechora, from the western, eastern and middle parts of the Ural mountain range; dotted line: squirrels only from the western slope; broken line: squirrels from the basin of the river Ob, Irtish and the vicinity of the town of Tomsk.

remainder flies away from the taiga and in its turn dies out in the places where it is forced to winter. Analogous phenomena embrace apparently a great part of Siberia as far as Yakutsk in the east. With our contemporary

knowledge of the cedar crops, it is not yet clear whether the phenomena described take place in the first year of a bad crop. On the other hand, it must be remarked that the conditions which are favourable to the increase of the squirrel and of the nutcracker are evidently rather similar and may, possibly to a great extent, consist in the state of the cedar nut crop, which determines a general raising of their number in these species. It is not clear as yet what is the character of the periodicity of the crop in other coniferous trees of the taiga; therefore it is difficult to say at present what part they play in regulating the numbers of the squirrel.

VIII. Summary.

1. The trapping of squirrels in Siberia and in the north-east of Europe, and also the statistics on the number of skins brought to the fairs during many decades, present an exact picture of the periodical fluctuations in the number of this rodent.

2. With considerable constancy, the decreases in the quantity of squirrel skins brought from the Northern Ural, Western Siberia and Jakutia, correspond to large emigrations of the Siberian nutcracker to the west, the south-west and partly to the south.

3. Sometimes the invasions of the nutcracker not only coincide with the year of a "bad squirrel harvest" but even precede it for a year.

4. The invasions of the nutcracker into Europe are due to a bad crop of cedar nuts in the native country of the bird; it is natural to suppose that the fall in the numbers of the squirrels primarily also depends in these regions upon the same failure of cedar nuts.

5. The years favourable to an increase of the squirrel and of the nutcracker coincide; it may be that here also there is a dependence upon good crops of the cedar nut, which permit the numbers of the population to rise rapidly.

6. The study of the biology and fruitfulness of the cedar, one of the most important food-yielding trees of the taiga, is the key to these ecological investigations in Siberia.

REFERENCES.

(A long enumeration of ornithological works, utilised by the author for the indication of the nutcrackers' invasions, has been omitted in order to reduce the length of the article.)

(1) **Blasius (1886).** "Der Wanderzug der Tannenhähner durch Europa im Herbste 1885 und Winter 1885–86." Ornis, 2, No. 4. (In German.)

(2) **Doppelmeyer, G. G. (1927).** "Fur hunting and trading of Jakutia." Collection of papers: "Jakutia," ed. U.S.S.R. Academy of Sciences. (In Russian.)

(3) **Gebler (1837).** "Uebersicht des Katunischen Gebirges." Mem. d. Kais. Akad. der Wissenschaft. vol. 8. (In German.)

(4) **Gorodkov, B. N. (1916).** "Observations on the life of the cedar in Western Siberia." Reports of the Bot. Mus. of the Acad. of Sciences, fas. 16. (In Russian.)

(5) **Grocholskaya (1929).** "The problem of the cedar nut." J. The business of oil-milling and the Fats, No. 3. (In Russian.)

(6) **Ivanov, V. A. (1929).** "The cedar trade of the Irkutsk province." Mem. East. Sib. Sect. of the Russ. Geogr. Society, vol. 5. (In Russian.)

(7) **Judanov, J. G. (1927).** "The Narym region. A geographical and trading sketch." (In Russian.)

(8) **Kokoulin, V. (1909).** "Information about the results of the work and of the researches in the districts of Vercholensk and Balagansk in the govt. of Irkutsk in 1908." (In Russian.)

(9) **Kozhantshikov, L. (1924).** "Trade hunting and fishing in the Minussinsk-taiga." Annual of the Minussinsk Museum. (In Russian.)

(10) **Morosov, F. (1914).** "The biology of our forest." (In Russian.)

(11) **Naumov, N. P. (1930).** "Materials for recognising the squirrel 'harvest.'" Reports on forest experimental work, No. 7.

(12) **Petrie, B. E. (1930).** "Hunting and reindeer-breeding of Tutur Tungus." (In Russian.)

(13) **Pogudin, A. A. (1930).** "Sketch of the trapping in the Kirensk circuit."

(14) **Pohle, P. P. (1913).** "On the biology of the Siberian Cedar." Mem. of St.-Petersbg. Bot. Gard. 13, Nos. 1–2.

(15) **Shuchov, J. N. (1928).** "Trapping in the northern part of the Tara district." (In Russian.)

(16) **Silantiev, A. A. (1898).** "Review of trapping in Russia." (In Russian.)

(17) **Slovtzov, J. J. (1892).** "The Vertebrates of the district of Tjumen and their distribution in the govt. of Tobolsk." Materials for a knowledge of the fauna and flora of the Russian Empire, No. 1.

(18) **Slovtzov, J. J. (1892).** "In the country of the cedar and of the sable." Memoir of Siber. Sect. of Russ. Geogr. Society, vol. 13.

(19) **Slovtzov, J. J. (1892).** "On the distribution and crop of the Siberian cedar." Ibid.

(20) **Soloviev, D. K. (1921).** "The Sajan trapping region and the sable trade there." (In Russian.)

(21) **Solskij, A. P. (1927).** "Forestry. Part I. The seeds of forest trees." (In Russian.)

(22) **Sonine, K. (1839).** "Some indications on the dominant species of forest trees in the district of Tsherdyn." Forest J. No. 3.

(23) **Sushkin, P. P. (1914).** "The birds of the Minussinsk region of Western Sajan and Urjanchaj land." Materials for a knowledge of the fauna and flora of the Russian Empire, No. 13. (In Russian.)

(24) **Troitzkij, N. V. (1930).** "The trapping in the Tshuno-Angara region." Memoirs of the Siberian regional hunting trade station. (In Russian.)

(25) **Walewsky (1875).** "The gathering of the Siberian cedar cones in the district of Verchotursk govt." Perm. J. of Forestry, Nos. 4–6. (In Russian.)

(26) **Zverev, M. D. (1930).** "Review of the rodents of the southern parts of the Minussinsk district and Chakassia (Siberia)." Zoological Magazine of the Middle Siberian State Geographical Society. (In Russian.)

BIRD POPULATION STUDIES: A PRELIMINARY ANALYSIS OF THE GOLD COAST AVIFAUNA

By J. M. WINTERBOTTOM, B.Sc.

(With two Maps in the Text.)

I. Introduction.

There is no need here to deal with the importance of a proper evaluation of the avifauna of a country, if its economic effects are to be computed. This has already been dealt with by Nicholson (6) and others. Nicholson also describes various methods of computing the bird population of a district. I shall here give an account of the results of some "travelling" and "stationary sample" censuses undertaken on the Gold Coast and compare them with similar censuses which I have taken in England.

Of all the methods of estimating bird populations, the most satisfactory, as a rule, is by making a direct count of the number of nests in a given area. But in tropical Africa there are several difficulties in the way of this being successfully accomplished. It demands more time than is usually available to a civil servant; dense thickets cannot be adequately searched, nor can forest trees or long grass; in forest country especially, there is no recognised breeding season. Finally, on a different line, the fauna is greatly augmented during the European winter and during the dry season in the Northern Sudan (which more or less coincide in point of time) by the immigration of migrant species, which must be ignored altogether if only nesting species are considered. For certain species, such as the palm and chestnut-and-black weavers (*Ploceus c. cullatus* and *P. castaneofuscus*), a direct census of breeding birds is probably feasible and would produce good results.

The travelling census method has been described in detail by Nicholson (7, 8). It is enough to say here that it consists in counting the numbers of the various species observed from a moving train or motor-car. The method has obvious disadvantages, especially in the forest region, but I do not propose to go into them in detail here. In a country like the Gold Coast, where the number of species is so large, it is necessary to resort to somewhat drastic grouping. In the forest, one's range of vision is very limited and the birds of the undergrowth and secondary thickets are practically unrepresented. Nevertheless, it does give a fair index of the relative abundance of the common species likely to be of economic importance, especially in the open country. The stationary sample method is simple and can be used to supplement the results of the travelling census. It is described later. I have used it only in the Accra residential area (see Map II), but I hope to use it extensively in Northern Rhodesia.

II. TRAVELLING CENSUS RESULTS.

Table I shows my full figures, unanalysed, for the whole of the Gold Coast, with my English figures for comparison. It will be noticed that the English average is much higher than the African, even in the gross figures. Actually these figures favour Africa, since the trains and cars normally attain considerably higher speeds at home than on the Gold Coast; the more frequent stops of the African trains (every train stops at every station) also tend to raise the level of the African figures, as compared with the European.

Table I. *Total figures, England and the Gold Coast, compared.*

Country	Mileage	Number	Average per mile	Dominant groups
Gold Coast	2700	19,457	7·2	Weavers (4703), Swallows (3839), Sparrows (1378), Bulbuls (1376)
England	2674	33,060	12·3	Rooks (8966), Starlings (8026), Sparrows (5180)

This collective number for the whole of the Gold Coast is not of much value as it stands, however. There are two sharply contrasted types of country in the colony, forest and open country (savannah). Table II shows the journeys analysed as far as possible and forest journeys separated from those of the savannah. In a few cases, where the journey was along a road passing continually from one to the other, any division of this sort has not been possible.

Turning to Table II, we see that the general figure for savannah country is decidedly higher than that for forest, the difference being 4·6 birds per mile. We should, perhaps, expect a difference, since the conditions of visibility are so poor in the forest, but nevertheless I think that more than this is needed to account for so marked a discrepancy between the figures. It is a commonplace that in England the avifauna of a large wood is poor, except on the borders, and I am inclined to attribute part of the difference to a definitely smaller population per unit area in the forest than in the savannah. H. W. Bates (**3**) and other travellers have commented on the rarity of birds and of animal life in general in tropical forests, and although their statements referred to the virgin rain forest, the same applies to some extent to the secondary forests that cover most of the area in which these counts were made.

Table II. *Gold Coast, forest and open country figures.*

Country	Mileage	Number	Average per mile	Dominant groups
Savannah	1083	10,768	9·9	Weavers (3416), Sparrows (1250), Swallows (1071), Bulbuls (852)
Forest	1508	7,989	5·3	Swallows (2619), Weavers (1578), Vultures (581)
Mixed	109	730	6·7	Weavers (263), Swallows (94)

Before proceeding to examine these figures in detail, however, a word must be said on grouping. For the purposes of these censuses, the following must be understood:

"Weavers"	means all species of the family	Ploceidae.
"Swallows"	" "	Hirundinidae.
"Swifts"	" "	Apodidae.
"Bulbuls"	" "	Pycnonotidae.
"Bee-eaters"	" "	Meropidae.
"Shrikes"	" "	Laniidae.
"Hawks"	" "	Falconidae (Bannerman's (1) use of the term, not Bates's (2)), except *Milvus*.
"Kites"	means only	*Milvus migrans*.
"Starlings"	means all species of the family	Lamprocoliidae.
"Hornbills"	" "	Bucerotidae.
"Pigeons"	" "	Columbidae.
"Coucals"	" "	genera *Centropus* and *Ceuthmochares*.
"Waders"	" "	family Charadiidae.
"Larks" includes, besides all species of the family Alaudidae, the pipits (Anthinae) also.		
"Kingfishers"	means all species of the family	Alcedinidae.
"Bushfowl"	" "	genus *Francolinus*.
"Herons"	" "	family Ardeidae.
"Terns"	" "	Sternidae.
"Cranes"	means only	*Balearica pavonina*.
"Pratincoles"	"	*Glareola pratincola*.
"Owls"	means all species of the order	Strigiformes.
"Woodpeckers"	" "	Piciformes.
"Quails" comprises *Turnix*, *Coturnix* and *Excalfactoria*.		
"Rollers"	means all species of the family	Coraciidae.
"Wagtails"	" "	genus *Motacilla*.

But the boundaries are not all as wide as they seem. For practical purposes, "Swallows" means *Hirundo rustica* in the forest and *H. senegalensis* and, to a lesser extent, *H. abyssinica*, in the open country. "Swifts" is practically confined to *Apus affinis* and *Cypsiurus parvus*, "Bee-eaters" to *Merops albicollis*, plus *Melittophagus pusillus* in savannah and *M. gularis* in forest country. The common "hornbills" are *Lophoceros semifasciatus* and, in dry areas, *L. nasutus*. "Pigeons," again, is represented mostly by *Streptopelia senegala*, *S. vinacea*, *S. semitorquata* and *Turtur afer*; "Coucals" by *Centropus senegalensis*; "Waders" by *Himantopus himantopus* and *Charadrius marminatus*; "Larks" by *Macronyx croceus* (Anthidae); "Bushfowl" by *Francolinus bicalcaratus*; "Herons" by *Ardea cinerea* and *Bubulcus ibis*; "Terns" by *Sterna albifrons* and *S. sandvicensis*; "Bulbuls" by *Pycnonotus barbatus*; and "Wagtails" by *Motacilla flava*. The only unwieldy groups are "Weavers," "Small Birds" and "Shrikes," and about these a few more words might be added.

The Ploceidae, as will be seen, are unquestionably the dominant family in the Gold Coast. Common species include *Ploceus cucullatus*, *P. castaneofuscus*, *Coliuspasser macrourus*, *Euplectes hordeacea*, *E. franciscana* and *Malimbus scutatus* amongst the Ploceinae, the first two being found all over the colony, the next three in the open country and the last in the forest; and *Spermestes cucullatus*, *Lagonosticta senegala*, *Vidua macroura* and *Estrilda astrild* amongst the Estrildinae. The only figures I have which bear on the relative abundance of these species of birds are those of a count of the males of *Euplectes* (both species together), *Coliuspasser*, *Vidua* and *Ploceus cucullatus*, made by my wife during a run from Accra to Aburi (22 miles) on August 31st, 1930. These are too small to be reliable, but I give them for what they are worth. They were: *Euplectes*, 16; *Coliuspasser*, 12; *Vidua*, 9; *Ploceus*, 5. In

the Accra residential area four species occur in my sample counts. They are, with figures, *Ploceus cucullatus*, 56; *Spermestes cucullatus*, 28; *Lagonosticta senegala*, 5; *Vidua macroura*, 1.

"Shrikes" comprises mainly three species: *Lanius collaris*, *Tchagra senegala* and *Laniarius barbarus*, but also includes *Dryoscopus gambensis* and *Lanius senator*. I have some figures bearing on the first three species, since I often kept them separately in my counts. They are: *Lanius*, 46; *Tchagra*, 34; *Laniarius*, 19.

Map I. Gold Coast Colony and Ashanti, showing census routes. The shaded portions represent forest country.

"Small birds" is a mere "waste heap," but is mainly composed of warblers (Sylviidae) and sunbirds (Nectariniidae). Of the warblers, *Cisticola*, with many species, is the most numerous genus, while *Cinnyris* includes most, but by no means all, of the sunbirds, *Anthreptes* being also important.

Finally, a word must be said on the ecological divisions of the country. For our purposes, we may regard them as two in number. Botanists have made many divisions (see, e.g., Irvine (4)), but an ornithologist can "lump" them into two big ones: "forest" includes the evergreen, deciduous and secondary forests of the botanist; "savannah" includes his savannah forest, tree savannah and grass savannah. The extent of each of these two divisions is indicated on Map I. The Northern Territories, in which I have taken no censuses, are not shown, but they consist entirely of savannah.

Savannah birds.

Even eliminating the forest areas, with their smaller figures, we find that the savannah average is definitely lower than that for England (9·9 against 12·3) and a difference of two and a half birds per mile in favour of the temperate zone causes surprise to those who think of the tropics as centres of luxuriant life. Why should this difference exist? We can rule out conditions of visibility, which are, if anything, better in Africa than in England. This means that there must be definitely fewer birds per unit area in Africa.

The limiting factor in any bird population may be one of three: food, nesting sites (and territories) or enemies. Normally, I think, one or other of the first two limits, since nesting sites, to be adequate, must be tolerably secure from enemies. The toll taken by enemies is less heavy when the birds have left the nest. In savannah country (but not, as is shown later, in the forest), food supply is probably the limiting factor. Food supply is increased by cultivation. It is to this that I attribute the denser English population. This may seem a bold statement, for even on the most arid plains insects are abundant. But many of these insects are not suitable food for small birds. Grasshoppers, one of the most numerous groups, not only present examples of protective and warning coloration, but are too unwieldy to form a good food supply for the smaller birds. Ants, again, are eaten regularly by only a few birds. Termites, although present in untold millions, keep to their earthy castles and only become available by accident. No doubt the seeds of grasses and fruits of trees form a plentiful source of food, but they are almost, if not quite, as rigid in their dependence on the seasons as are similar food resources in Europe. Cultivation increases the food supply indirectly by making it more available and directly by the crops themselves (e.g. maize, millet, rice), and by their parasites (e.g. caterpillars). There are, of course, exceptions: for instance, I have noticed that most birds do not like the dense shade of cacao plantations, and this is confirmed by the very low figure (2·1 per mile) obtained for a run of 25 miles between Mangoase and Nsawam where the line passes through an almost continuous series of cacao farms. The cacao is, of course, an alien tree and produces and supports practically nothing of food value to the local birds.

This surmise as to the effects of cultivation is supported by two sets of figures, too small to dogmatise about, but nevertheless suggesting that the explanation here offered is the right one. On the Accra plains, I particularly noticed that the land along the railway from Accra to Weija was relatively very highly cultivated. The Government sisal plantation and many native farms lie here. The figures for five runs over part or the whole of this distance and aggregating 35 miles, gave an average per mile of 22·2, which is very much higher than that for savannah country in general. Again, the Accra plains north and north-east of Accra and the Togoland savannah country are

more thickly populated and therefore more cultivated than the savannahs of Northern Ashanti. If we compare the results of censuses between Accra and Nsawam and Accra and Ho on the one hand with those between Ejura and Bantama and Ejura and Borku *via* Wenchi on the other, we find:

Table III. *Accra-Togo plains and Northern Ashanti compared.*

District	Mileage	Number	Average per mile
Accra-Togo	802	8791	10·9
Ashanti	186	1133	6·1

We see from this that the Accra-Togoland region has a bird population somewhat in excess of the average for savannah in general (1 per mile), while the savannahs of Northern Ashanti are markedly less densely populated (nearly 4 per mile less). This is what we should have expected from the conditions set out above. I have deliberately excluded the results of two censuses along the coast between Accra and Prampram because they run through less populated areas than the others. They tend to support the hypothesis also, the figures being 484 birds in 57 miles, average 8·5.

In Table IV we see the figures analysed from the point of view of season. It will be seen that in savannah country the average is slightly less for the wet season than for the dry. This is to be expected when we remember that the dry season in the main corresponds to the European winter and that consequently there is an influx of birds from Europe and also, be it noted, from the borders of the desert. As far as the savannah is concerned the latter group of immigrants are probably the more important. The question of seasonal fluctuations and its bearings will be discussed more fully below, when we come to deal with the birds of the forest, where the difference in population is so much greater.

Table IV. *Seasonal figures, travelling census.*

	Forest			Savannah			Total		
Season	Miles	Number	Avge	Miles	Number	Avge	Miles	Number	Avge
Dry	349	2983	8·5	417	4239	10·2	766	7,222	9·4
Wet	1159	5006	4·3	666	6529	9·8	1834*	12,256*	6·6

* Includes figures for 109 miles of mixed savannah and forest.

Note. "Dry" is December–April and August; "Wet," May–July and September–November. In the forest, April and perhaps March are also wet, but at Accra in 1930 the rains did not set in until May and all April figures refer to this area.

It is often considered that the number of birds seen depends considerably on the time of day at which the counts are taken and Table V lends support to this view, at least for the savannah. The forest figures are too small to be reliable. It might, perhaps, be argued from this that only these early morning figures should be considered when we are comparing the faunas of England and the Gold Coast. But the same thing occurs, though to a lesser degree, in England. Moreover, even these, the most favourable Gold Coast figures, only

give an average about equal to the total for all the English figures together, irrespective of time, place or season. So that the conclusions arrived at above cannot be considered as invalidated by this criticism. The dominant group throughout is the weavers.

Table V. *Effect of time of day upon census figures.*

Time	Mileage	Total	Average per mile	Dominant groups
Early morning (7–9)	233	2980	12·7	Weavers (1135)
Midday (11–2)	226	2047	9·1	Weavers (657)
Evening (4–6)	234	2464	10·5	Weavers (828)
Early morning	51	866	17·0	Swallows (631)
Midday	173	1953	11·3	Swallows (539)
Evening	146	1062	7·3	Weavers (261), Swallows (175)

Note. The first three lines refer to savannah country, the last three to forest.

Coming now from the general to the particular, let us consider the composition of this savannah bird association. Its weavers I have already dealt with. They are the dominant group and fill the place occupied in Europe by the finches. They are, however, even more vegetarian, for even the young, which in finches are fed as a rule on insects, in weavers are normally fed on grain and seeds[1]. Still, even these strict vegetarians sometimes take animal food, for I have notes of two species of *Ploceus* which I have seen eating winged termites. Sparrows, swallows and bulbuls are other big groups. The sparrow (*Passer g. griseus*) is the only member of the Fringillidae (if it be a member of this family, which some systematists dispute) that competes really successfully with the weavers, and even it can only do so in the neighbourhood of towns and villages. The lively, cheerful bulbul (*Pycnonotus barbatus inornatus*), while profiting by the presence of man, is much better able to make a living in his absence than is the sparrow. The bulbul is a bird of the trees and bushes, however, and this, together with its inconspicuous coloration, probably causes many to be missed on census runs.

Forest birds.

The forest figures present marked differences from those for the savannah. Table II shows that the average number of birds seen per mile is much smaller, and I have discussed why this should be so. But a glance at Table IV shows that there is more difference between the averages for the wet and dry seasons in the forest than there is between dry season forest and savannah averages. This is a remarkable fact. It is still more remarkable that it should be in the dry season, when insect and plant life is at its lowest ebb, that this extra host, doubling the observed population, should be borne. Examination shows that this increase is due, almost entirely, to the influx of European swallows (*Hirundo r. rustica*), although other migrants, notably the yellow wagtail (*Motacilla flava*), black-crowned bee-eater (*Merops albicollis*) and buff-backed

[1] There are some weavers which are insectivorous (e.g. *Malimbus* spp.), but they are forest forms.

heron (*Bubulcus i. ibis*), play a minor part. The question at once springs to mind: if the forest can support all these extra birds in the dry season, why should it not do so in the rains also? The answer, as it seems to me, is that it can. Clearly the controlling factor cannot be food, which is more abundant in the wet season than in the dry, at least so far as insects are concerned. And it is insects that form the diet of the four species mentioned above, as well as of the various warblers and other species that come in at the same period. If food is not the controlling factor, what is? The most probable is, in my opinion, nesting sites. We know that this is the limiting factor in the abundance of many hole-nesting species in temperate lands. In the tropics, good, safe nesting sites must be still more difficult to find. Such insidious enemies as snakes and ants must be avoided and not all birds possess the address of those species of woodpeckers which Bates reports (**2**) as digging out nesting holes inside the nests of ants! Moreover, the young of many birds suffer greatly from the heat, and this may be an additional factor rendering many otherwise suitable nesting sites untenable. That the Palaearctic migrants originated in the south and spread northwards as the Pleistocene ice sheet shrank is the most plausible hypothesis. They went north to breed and they did so, not because food was short, but because they could find no suitable nesting sites elsewhere. The "best" birds took what sites there were and the others were pushed out. This supports the opinion Mr F. Finn has often expressed to me—that the temperate regions are inhabited by the tropical failures. But this only applies to forest regions. The open country conditions are far more like those of temperate regions, with the result that here we often find the instinct for the establishment of breeding territories, necessary to safeguard the food supply of the young broods.

Apart from these striking migration figures, the forest groupings differ chiefly in the increase of hornbills and of vultures, the latter being more or less fortuitous, since the vulture happens to be rare on the Accra plains; and in the decrease of nearly everything else. The groups themselves are often represented, wholly or in part, by different species, as has already been indicated. But it is astonishing how the really common birds are found everywhere. The only exception seems to be the "toucan" hornbill (*Lophoceros semifasciatus*). A moment's thought, however, gives a convincing explanation. The sparrow, bulbul, crow, vulture, little swift and palm weaver (*Ploceus c. cucullatus*) all profit by man's presence and productions; the swallows and bee-eaters have found that telegraph wires make better look-out perches than those provided by nature. In a relatively densely populated country like the Gold Coast, the common birds must be those that can tolerate man or turn his works to their advantage, and these birds are mainly the same all over the country. The less adaptable forms must retreat before the advance of cultivation. Formerly these may have been the dominant species. Now, however, man puts a premium on brains and the slower-witted birds are

killed off. These travelling censuses reveal one stage of the formation of a man-bird ecological association: the next section, in which the sample census results are discussed, shows this process carried a stage further.

Two other points need to be mentioned briefly before passing on. Table VI gives figures showing the proportion of birds of prey to the total of all birds observed, both on the Gold Coast and also, for comparative purposes, in England. In the Gold Coast figures, the column "Hawks" includes all members of the Falconiformes except *Necrosyrtes monachus*, plus two owls: in the next column, the Laniidae are included also. Thus almost all the birds that eat other birds are included, but it must not be forgotten that in most cases, birds are not the staple diet of these groups, whose members feed mainly on mammals, lizards and insects. The English figures include hawks and owls only, and most of the hawks were kestrels (*Falco tinnunculus*). That our English avifauna was impoverished has long been known, but that hawks should be reduced to one-tenth of their numbers under more natural, if climatically different, conditions is somewhat surprising.

Table VI. *Proportion of birds of prey to other birds.*

Country	(1) Hawks	(2) All birds of prey	(3) All birds	Col. 1 / Col. 3	Col. 2 / Col. 3
Gold Coast	237	375	19,487	1 : 82	1 : 52
England	36		33,060	1 : 918	

Finally, it must be remembered that nocturnal birds are rarely or never represented in these censuses. Two groups of these, the owls and the nightjars, are of considerable economic importance, however. In one run of 7 miles along the Accra-Dodowa road in March, 1930, about midnight, I counted 14 nightjars (*Scotornis climacurus* and *Macrodipteryx longipennis*), which suggests that these birds are decidedly numerous. *Scotornis* certainly breeds on these plains, but its numbers are probably augmented by dry season immigrants, while the standard-wing reaches Accra in the dry season also, but is not recorded as breeding there.

III. Sample census results.

So much, then, for the avifauna of the Gold Coast as a whole. Let us now consider that of the Accra residential area, as revealed by the stationary sample method, in more detail. Accra is built on a normal and unremarkable piece of the coastal plain. This plain is an arid area with a flora composed mainly of grasses. Scattered trees, mainly baobabs (*Adansonia digitata*) and *Elaeophorbia drupifera*, and patches of thorny scrub also occur, the latter especially becoming more numerous as one goes inland, where the oil-palm (*Elais guinensis*) also occurs; while farms of cassava and, more rarely, maize, occupy an appreciable part of the area close to the town. The plains are ravaged by annual grass fires.

The "Ridge" flora is derived in part from that of the plains and in part from introduced plants, with a few weeds of cultivation in addition; of these *Commelina nudiflora* is the most conspicuous. Probably owing to the absence of fires, but perhaps owing also to the watering of flower beds, the "Ridge" supports far more trees than the plain proper. Nearly all of these are aliens, however. The most important and most numerous are the nim (*Azadirachta indica*), the fruit of which is eaten by bulbuls, thrushes, etc., the cassia (*C. Siamea*), the mango (*Mangifera indica*), the flamboyant (*Poinciana regia*) and the whistling pine (*Casuarina equisetifolia*); others include the Indian almond (*Terminalia catappa*), the tulip tree (*Spathodia campanulata*), whose flowers are so attractive to sunbirds, and the teak. Shrubs important to sunbirds and others include the milk-bush (*Thevetia neriifolia*), pride of Barbados (*Caesalpinia pulcherrima*) and species of *Allamanda* and *Hibiscus*. Corallita (*Antigonon leptopus*) and morning glory (*Ipomoea digitata*) are climbers which supply suitable nesting sites for small birds.

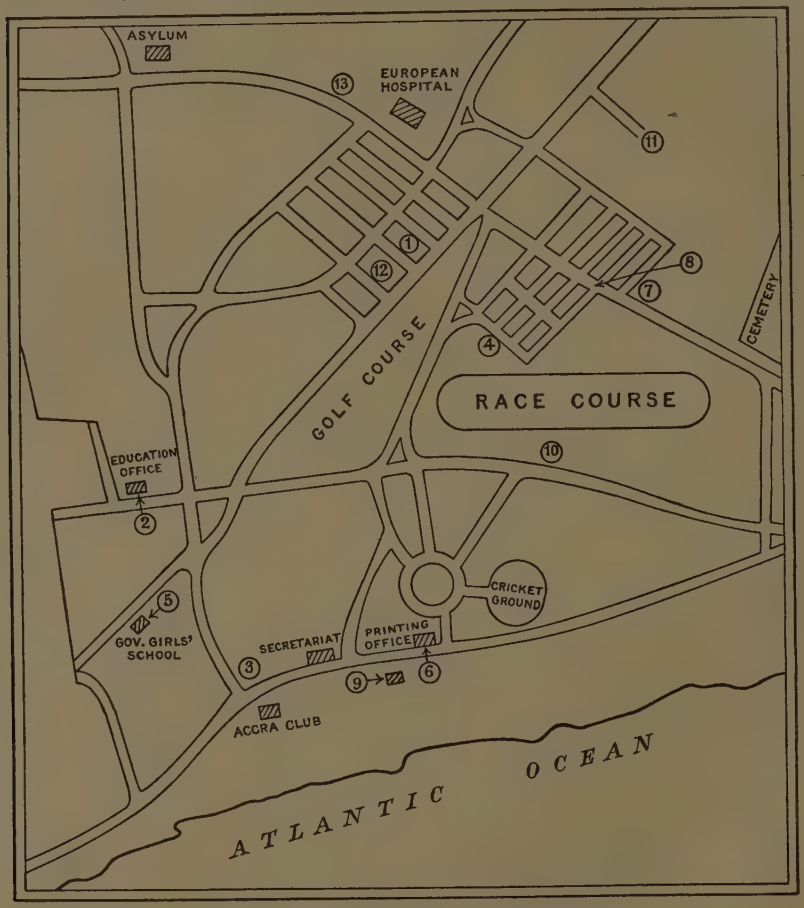
The residential ridge falls into three divisions. The southern section comprises the area between the lowermost east-and-west roads (see Map II) and the bungalows and compounds adjoining. The central area runs in a T-shaped piece down between Accra and Christiansborg and across the middle of the amp, by way of the racecourse and the Victoriaborg golf course to the African suburb of Adabraka. The vegetation is mainly grass, which, however, is never allowed to become really long before being cut down by gangs of prisoners or sanitary labourers. The northern section, where most of the Europeans live, consists of a Western Ridge, an Eastern Ridge and the Dodowa road between the two. Traders' houses stretch along the Dodowa road right up to the edge of the map or further.

The sample census method is very simple and gives a finer approximation than the travelling method. Over a given area, a number of points are taken and at each a note is kept of the different species seen or heard during a short time (say 5 or 10 min.). By making the number of counts large and the time of counting short, the common species are seen more often than the less common. It is a method with obvious defects, but it enables an approximate picture to be obtained of the avifauna of a given ecological area with far less time and trouble than would be demanded by a full census.

Thirteen stations were taken, more or less at random, for sample counts. Ideally, of course, the same number of counts should have been taken at each, but this was impossible. A few notes on each station follow.

(1) "Fourth Road," was my own bungalow. More counts were taken here than at any other single station. It is a typical situation for the West Ridge, where the bungalows are smaller and closer together than elsewhere. 45 counts. (2) "Education Office," lies on the extreme western edge of the area. For obvious reasons, it was impossible to spend time and attention in making systematic counts, but casual observations were noted each day. 31 counts.

(3) "Accra Club," was really a bungalow opposite. Seven counts. (4) "Racecourse," was a plantation of whistling pines between the racecourse, Sixth Road and Maxwell Road. As related elsewhere (**10**) I suspect that the Eritrean shikra (*Accipiter badius sphenurus*) nested here. Seven counts. (5) "Girls'



Map II. Accra. European residential area.

School," was very similar to No. 2. Nine counts. (6) "Printing Office," needs no comment. Two counts. (7) "Castle Road, East," is the extreme end of the Eastern Ridge, looking over the grassy country to Christiansborg and the cemetery. Five counts. (8) "Third Avenue," is a typical Eastern Ridge site, at the junction of Third Avenue and Castle Road. Five counts. (9) "Police Station," was the centre of the main residential area. Six counts. (10) "Rowe

Road, East," was for the southern section what No. 7 was for the northern. Seven counts. (11) "Tenth Road," was the only station in the northern and most recently built section of the residential area. It and No. 13 were the only ones which gave any view of relatively untouched "bush." Four counts. (12) "Second Road," was very similar to No. 1, but also gave a view of the golf links. Seven counts. (13) "Hospital," was for the western side what Nos. 7 and 10 were for the eastern. It gave a view over a gravel pit, cassava farms and "bush," besides the compounds of the European Hospital and two bungalows. Three counts.

In all 138 counts were made. The species observed were found to number 35 (cf. Ipswich, England, with 28 species for 108 counts spread over three months). In these censuses, ear may be more valuable than eye, at least for some species, such as *Turdus libonyanus* and *Lampromorpha caprius*, which keep very much to cover. Table VII gives a list of the species observed, in numerical order.

Table VII. *Species observed in sample counts, Accra.*

Position	Species	Credit index	Number
1	Passer griseus griseus	1	137
2	Pycnonotus barbatus inornatus	1	128
3	Micropus affinis affinis	2	84
4	Streptopelia senegalensis senegalensis	3	64
5	Ploceus cucullatus cucullatus	3	56
6	Turdus libonyanus saturatus	3	49
7	Cinnyris cupreus cupreus	3	48
8	Cisticola sp. inced.	3	45
9	Motacilla flava subsp.	3	42
10	Pogoniulus chrysoconus chrysoconus	3	41
11	Corvus albus	3	36
12	Spermestes cucullatus cucullatus	4	28
13	Halcyon chelicuti chelicuti	4	27
	Accipiter badius sphenurus	4	27
15	Lampromorpha caprius	4	23
16	Eremomela pusilla pusilla	4	20
	Cinnyris coccinigaster	4	20
18	Cypsiurus parvus brachypterus	4	14
19	Milvus migrans parasiticus	4	11
20	Merops albicollis	4	9
	Tchagra senegala pallida	4	9
22	Muscicapa striata	4	7
23	Lagonosticta senegala	4	5
24	Hirundo senegalensis saturatior	4	4
	A Wader, sp. inced.	4	4
26	Sp. inced. ("Bicycle-bird")*	4	3
27	Buteo auguralis	5	2
	Elanus caeruleus caeruleus	5	2
	Streptopelia vinacea vinacea	5	2
30	Cuculus canorus subsp.	6	1
	Macronyx croceus croceus	6	1
	Necrosyrtes monachus monachus	6	1
	Saxicola rubetra rubetra	6	1
	Turtur afer afer	6	1
	Vidua macroura	6	1

* The bird called "Bicycle-bird" I never saw, and the name here applied to it is a private one. It was possibly a shrike of the genus *Dryoscopus*.

The credit index is obtained as follows:

Credit index of	1	means that a bird occurs in	75 per cent. or more counts.
,,	2	,, ,,	over 50 per cent. but less than 75 per cent.
,,	3	,, ,,	over 25 per cent. but less than 50 per cent.
,,	4	,, ,,	over 2 counts but not less than 25 per cent.
,,	5	,, ,,	2 counts only.
,,	6	,, ,,	1 count only.

The list reveals marked differences from the general avifauna of savannah country as computed by the travelling census method. In part, this may be due to the more accurate picture given by the sample method, especially in its inclusion of the shyer birds. But this can only explain a relatively trivial part of the difference and we must conclude that the difference of conditions has evoked a radical change in the bird life also. Of the weavers, the dominant savannah group, only *Ploceus cucullatus* and, to a much lesser extent, *Spermestes cucullatus*, are really numerous. The widespread and successful savannah species, *Euplectes h. hordeacea*, *E. franciscana* and *Coliuspasser macrourus*, are not represented at all. The dominant species are the grey-headed sparrow (*Passer g. griseus*) and the black-headed bulbul (*Pycnonotus barbatus*), which both have credit indices of 1; with the little swift (*Apus affinis*), credit index 2, and the laughing dove (*Streptopelia s. senegalensis*), credit index 3, as next most numerous. Except for the bulbul, I should hesitate to describe any of these species as numerous in the "bush." The 1250 sparrows in the last column of Table II were almost all seen close to towns and villages, and a glance at the Appendix will show that pigeons, again, play a smaller part in the bird life of the Colony than would have been assumed had these Accra figures been the only ones available. The same applies to swifts, with the added force that, away from a few towns, *Cypsiurus parvus* is a much commoner bird than *Apus affinis*. The 103 swifts seen between Wenchi and Borku (20 miles) on September 27th, for instance, were all palm swifts. The abundant swallows of the bush are represented by casual foragers in the town. Even the common hawk is different: in the bush it is *Elanus caeruleus*, which occurs in only two sample counts in the town, where the most abundant raptor is a small hawk, probably the Eritrean shikra (*Accipiter badius sphenurus*).

These counts were all taken between March 1st and April 10th, except for one made in mid-February. They can be taken as giving a fair index of the bird population at the end of the dry season, but it remains to be seen to what extent this is modified at other times of the year. Wagtails (*Motacilla flava*), bee-eaters (*Merops albicollis*), whinchats (*Saxicola rubetra*), and perhaps black kites (*Milvus migrans*) may have begun their northward migration. *Ploceus c. cucullatus* had begun nest-building, if not breeding. So, too, had *Turdus libonyanus*, whose song caused its presence to be known many times when the bird itself was invisible. *Lampromorpha caprius* was recognised only just after these censuses had begun, so that I have no idea whether its numbers fluctuate with the season and I do not know anything of its status in the open bush.

Summing up, we may call the first three species "dominant," the next eight (4–11) "common," the next six (12–17) "fairly common" and the remainder "visitors" of varying status, some being numerous in the open country adjoining the ridge. The presence of houses has operated to the advantage of Nos. 1–4 and 11, houses and trees to the advantage of No. 5 and trees to that of Nos. 6 and 15. The trees have lessened the numbers of *Cisticola*, *Hirundo*, *Elanus*, *Macronyx* and *Saxicola* and have been agents in the total exclusion of *Euplectes* and *Coliuspasser*. In this way the original savannah fauna has become modified. Each town modifies the local fauna in its own way, so that the fauna of any town depends on two factors, the fauna of the surrounding country and the conditions in the town itself. For instance, I kept a list of the birds noticed at Freetown, Sierra Leone, when the ship called there on the way home on April 14th. The total number of species noted was 17, one of which I failed to identify. Of the others, only seven appear on the Accra list at all, namely: *Necrosyrtes monachus*, *Milvus migrans*, *Hirundo senegalensis*, *Cinnyris coccinigaster*, *Pycnonotus barbatus*, *Corvus albus* and *Apus affinis*. Six others I have seen at Accra, but not when census-taking and not all of them in the residential area: *Larus fuscus*, *L. cirrhocephalus*, *Sterna hirundo*, *S. sandivicensis*, *Halcyon senegalensis* and *Bubulcus ibis*. The others were *Cinnyris verticalis*, *Spermestes fringilloides*, *Gypohierax angolensis* and a shrike of some sort. Freetown favours vultures, kites and seabirds; moreover, the heavy rainfall and the effect of this on the surrounding country results in the available fauna being different also. In Lobito, again, where the ship I was in called on August 10th, I noted 15 species, of which three only (*Passer griseus*, *Streptopelia senegalensis* and *Cypsiurus parvus*) were identical with Accra birds, while one other (a wader) may have been. *Hirundo*, *Macronyx* and *Pycnonotus* were represented by allied species. *Sterna sandvicensis*, which is on the Freetown list, was represented, as were *Phalacrocorax lucidus* and *Ceryle rudis*, which I have seen in Accra, but not while census-taking. Of the others, two (*Moris capensis* and *Phalacrocorax capensis*) were southern species, one (a pipit) was a bird of arid soils and the other two (*Ardea cinerea* and *Egretta garzetta*) were marsh birds, which occur on the Gold Coast in suitable localities.

Compared with my English results, the Gold Coast sample counts show a much wider scattering, since no less than 11 species have a credit index of 3 or better. Accra is, however, a less severe environment than Ipswich. I have suggested above that the popular conception of the tropics as centres of luxuriant bird life is a wrong one. This is true so far as gross numbers are concerned. But in variety of species the tropical regions are supreme. In Switzerland, for instance, about 170 species can be regarded as common at some time or other during the year (**9**); Kirkman (**5**) includes 187 species in his little book on common birds of the British Isles, but some of these are only common in very restricted localities. For the Gold Coast, I have notes

on about 170 species in 18 months, besides having seen about 20 more that I could not identify; yet I had hardly begun to know the forest birds and had not touched the Northern Territories; I included no rarities among the species dealt with. All three countries have towns and cultivation, virgin forest and grassland, rivers and lakes. England and the Gold Coast have sea-coast, England and Switzerland mountains. All have their winter visitors, but the number of summer visitors to the Gold Coast is insignificant—only one (*Larus cirrhocephalus*) being included in my notes (**10**).

IV. Summary.

1. Bird censuses from the train indicate a lower bird density in Nigeria than in England, and lower density in forest than in savannah.

2. The characteristics of the bird life of savannah and forest are described; the comparatively high abundance of hawks in Nigeria is striking.

3. A sample census was taken at various points in the town of Accra, for comparison with the savannah.

V. Acknowledgments.

I have to acknowledge my indebtedness to Mr E. M. Nicholson and to Prof. J. S. Huxley for valuable advice on the arrangement and presentation of the material here set forth, but they must not, of course, be held in any way responsible for its blemishes; and to my wife for preparing the maps from my rough sketches.

References.

(1) **Bannerman, D. A. (1930).** "The birds of tropical West Africa." Vol. 1.
(2) **Bates, G. L. (1930).** "A handbook of the birds of West Africa."
(3) **Bates, H. W. (1863).** "A naturalist on the Amazon."
(4) **Irvine, F. R. (1931).** "Plants of the Gold Coast."
(5) **Kirkman, F. B.** "British birds."
(6) **Nicholson, E. M. (1927).** "How birds live."
(7) **Nicholson, E. M. (1928).** Discovery, 104, 253–7.
(8) **Nicholson, E. M. (1929).** "The study of birds."
(9) **Studer, T.** and **von Burg, G. (1916).** "Liste distributive des oiseaux de la Suisse."
(10) **Winterbottom, J. M.** "Field notes from the Gold Coast." Ibis. (In press.)

APPENDIX.

Totals of all birds observed in travelling censuses, Gold Coast.

Position	Species	Number
1	Weavers	4703
2	Swallows	3839
3	Small birds	2601
4	Sparrows	1378
5	Bulbuls	1376
6	Vultures (*Necrosyrtes monachus*) ...	849
7	Crows (*Corvus albus*)	752
8	Swifts	744
9	Hornbills	563
10	Pigeons	401
11	Bee-eaters...	303
12	Wagtails	181
13	Hawks	177
14	Starlings	169
15	Herons	152
16	Shrikes	138
17	Terns	129
18	Waders	92
19	Kites	60
20	Larks	58
21	Kingfishers	57
22	Cuckoos	25
23	Bushfowl	24
24	Woodpeckers	22
25	Thrushes	13
	Touracos	13
27	Piapacs (*Ptilostomus afer*)	10
28	Pratincoles	7
29	Rollers	6
30	Coursers (*C. temminckii*)	2
	[illegible]	2
	Quails	2
33	Bustard (*Lissotis melanogaster*)... ...	1
	[illegible]	1
	Darter	1
	Parrot	1

STUDIES OF FLUCTUATIONS IN INSECT POPULATIONS

II. THE INFESTATION OF MEADOW FOXTAIL GRASS (*ALOPECURUS PRATENSIS*) BY THE GALL MIDGE *DASYNEURA ALOPECURI* (REUTER) (CECIDOMYIDAE)

By H. F. BARNES, M.A., Ph.D.

(*Entomology Department, Rothamsted Experimental Station.*)

CONTENTS.

		PAGE
I.	Introduction	98
II.	Methods	100
III.	Identification and biology	100
IV.	Degree of infestation of the grass	101
V.	Degree of relative parasitism of the midge	103
	(i) Identification	103
	(ii) Methods and results	103
VI.	Emergence	104
VII.	Sex ratio of *D. alopecuri* (Reuter)	107
VIII.	Summary	108
IX.	Acknowledgments	108
	References	108

I. Introduction.

Before going any further it may be as well to state again the object of these studies. It is primarily to collect information regarding periodic fluctuations as they occur in nature and, secondly, to provide hints of the factors involved. Subsidiary studies based upon the latter are intended to accompany the main work. The third of these, "A study of the segmentation of the antennae in gall midges," has recently been published (5). In this it was shown that in some species and genera food affects the size of the adult midge only; and that in others it affects the size of the adult midges and, in addition, the number of antennal segments. The ultimate aim of the whole project is to enable one to predict outbreaks of insect pests. This can only be done when, having developed suitable technique for studying such phenomena, one knows the manner in which the insect population varies from time to time and the causes of such fluctuations.

The first study (4) in this series dealt with the wheat blossom midges as they occurred over the period 1927–31 in a field (Broadbalk) of permanent wheat. It was shown that there were certain fluctuations during this period both in the degree of infestation of the wheat by the larvae and in the degree of parasitism. Further, it was obvious that the technique employed required

amplification and modification in certain respects. Owing to the interesting results which had already appeared, e.g. a possible periodicity in fluctuations (6), it was decided to continue this particular study for a further period of five years. Full discussion of the results was held over until other similar studies had been made.

The present paper deals with the infestation of wild Meadow Foxtail grass (*Alopecurus pratensis*) by the gall midge *Dasyneura alopecuri* (Reuter). This study resembles the previous one in that the same three aspects have been taken into consideration, viz. the degree of infestation of the crop, the degree of parasitism and the dates of emergence of the adults. Further, the period during which the work has been in progress has been practically the same, 1927–32.

The method of taking samples of wild populations, in the fully fed larval stage and of rearing the adults in an outdoor insectary, has also been nearly identical. However, instead of extracting the larvae from the plant and placing them in lamp glasses over pots containing fibre and soil, the grass heads containing the larvae have been placed in lamp glasses over pots containing soil alone. This is merely an item of breeding technique; in cases where the larvae normally leave their host plant to winter in the soil, fibre is used on account of its non-moulding and its good retention of moisture; in cases where the larvae remain in their host plant and where the particular part of the plant which contains the larvae normally falls to the ground, e.g. grass seeds or florets, the material is placed on soil alone.

There is one other important difference in this study compared with the former one which should be pointed out here. The samples of grass have been collected near Aberdeen in July and August and then kept at Harpenden throughout the following winter, spring and early summer. Thus the midges have spent the adult, the egg stage and the growth period of the larvae under the climatic and other environmental conditions pertaining to the Aberdeen district. The developmental period of the larvae and the pupal stage has been spent under Harpenden conditions. In the previous study the whole life of the midges was spent under Harpenden conditions, first on Rothamsted farm and then in the insectary at Harpenden. One effect of this change of climatic conditions has been shown (1) to cause the emergence of the midges at the normal time of that locality in which they have been kept since becoming full grown, i.e. the Aberdeen midges will emerge at the normal date for Harpenden, not Aberdeen. This, however, only holds good when the time spent in the new locality is considerable. For example, samples of grass containing the summer brood of *Stenodiplosis geniculati* Reuter, another Meadow Foxtail grass midge, when brought from different counties, emerged at dates presumably corresponding to those of the various localities (*loc. cit.* p. 352). This was owing to the fact that they were only in the new locality (Harpenden) for a few weeks.

The object in obtaining the sample from Aberdeen was twofold. Firstly, the foxtail grass at Aberdeen had been found to contain the larvae of *D. alopecuri* alone, if collected at the end of July or early August, and so the samples would not be contaminated by either of the other two Meadow Foxtail midges, *Contarinia merceri* Barnes and *Stenodiplosis geniculati* Reuter. Secondly, it was desired to see whether it would be possible for headquarters to instruct satisfactorily persons at outside centres when and how to collect samples and send them in to the centre of operations. If no untoward difficulties arose either owing to the administration or to the effect on the insects, such a procedure would increase enormously the scope of the main study.

II. Methods.

Owing to the kindly co-operation of Dr Guy Morison, who collected the samples at specified dates, the material was obtained from two spots, only a few miles apart, along the Aberdeen—Newburgh road in late July and early August. This period was fixed for two reasons: firstly, by that date any *Contarinia merceri* larvae would have left the grass heads for the soil and so, no *Stenodiplosis geniculati* being known to occur in that locality, the sample would contain only the one species of midge it was desired to study; the second reason was that by that date the midge larvae should have finished their actual growth period.

Samples of roughly 100 heads of wild hedgerow Meadow Foxtail grass were collected and sent to Rothamsted. Here the packages were opened and if the florets were still on the heads, 100 heads were counted out and placed in a lamp glass over a pot containing soil. If, on the other hand, the florets owing to ripeness or dryness had fallen off the stems by time the packages had arrived, the whole sample was put direct into the breeding cage, merely noting how many heads had been put in. The breeding cages were then placed in the outdoor insectary on the same shelf as all the other material used in this series of studies.

In the following early summer the midges and their parasites were collected and counted, day by day, as they emerged. In this way the following data have been obtained: (1) the degree of infestation of the crop from year to year, (2) the degree of relative parasitism, and (3) the comparative dates of emergence. The method is simple and could be carried out by any one with very little practice.

III. Identification and biology.

In most districts in Great Britain three species of gall midges are to be found in the heads of Meadow Foxtail grass. Keys for their separation are included in a recent paper on their biology (**1**). There is no need to repeat here any more than a very brief résumé of the life history of the particular midge in question.

Dasyneura alopecuri (Reuter) has normally only one brood a year (certainly only one in Aberdeen), the adults being on the wing from late April till the third week in July, the maximum numbers occurring from about May 28th to June 17th. Eggs are laid very soon after emergence and the larval growth period usually is completed towards the end of July, i.e. by time the florets of the grass start falling to the ground. The fully grown larvae remain in the seed cases on the ground as developing larvae until the following May when pupation, quickly followed by emergence, takes place.

IV. DEGREE OF INFESTATION OF THE GRASS.

In contrast to the previous study on the wheat blossom midges where the degree of infestation of the crop was based on actual counts of the numbers of larvae present in 500 ears of wheat, it was decided in this case to calculate the infestation by the number of midges and parasites emerging the subsequent year. These figures, when corrected to allow for mortality, due to faulty technique in breeding during the winter months, should give a fairly accurate figure for the infestation. It had been found previously (1) that 75–84 per cent. emergence of midges took place when the samples were kept in the insectary. Supposing, therefore, that the observed figure of midges and parasites was 80 per cent. of the total present, we can estimate the total infestation of larvae the previous year. It is presumed that one parasite only comes to maturity out of each midge larva and also that the mortality due to faulty breeding technique would be the same each winter. As one larva destroys one seed we know how many seeds are destroyed, and if we know the average number of seeds or florets per head of grass we could calculate the percentage seed lost. From previous work it is known that on the average 287 florets occur in each ear of grass in the particular Aberdeen locality. Supposing seven of these florets would normally (and quite apart from midge attack) remain blind and fail to produce seed, we get the figure of 28,000 seeds for 100 heads of grass.

Table I shows the degree of infestation in the two localities over the period studied worked out on this basis.

The first year written in the first column indicates the year the sample was picked, i.e. the year the damage was done, and the second year in the same column means the year the midges emerged as adults and were ready to start a new infestation.

It will be seen at a glance that in the summer of 1928 there was the largest attack recorded, 22–35 per cent. of the seed being lost. At the same time the proportion of midges reaching maturity the following year (1929) compared with the number of parasites was extraordinarily high. At locality A the number of midges had increased at least threefold, while the number of parasites had decreased more than eightfold. A suggested explanation for these changes is given later on in this paper in section VI, "Emergence." In

Table I. *Degree of infestation of Meadow Foxtail grass in two localities (A and B) near Aberdeen*, 1927–31.

Year	Number of midges emerged from 100 heads of grass	Number of parasites emerged from 100 heads of grass	Total emergence	Total infestation = seeds lost in 100 heads of grass (estimate)	% crop lost (estimate)
		Locality A.			
1927–28	1498	924	2422	3028	11
1928–29	4748	114	4862	6078	22
1929–30	1366	312	1678	2098	7
1930–31 (i)	727	328	1055	1319	5
(ii)	1202	339	1541	1926	7
1931–32 (i)	1076	33	1109	1386	5
(ii)	1355	43	1398	1748	6
		Locality B.			
1927–28	—	—	—	—	—
1928–29	7565	216	7781	9726	35
1929–30 (i)	2540	16	2556	3195	11
(ii)	1099	12	1111	1389	5
(iii)	885	4	889	1111	4
1930–31 (i)	1892	74	1966	2458	9
(ii)	2016	121	2137	2671	9½
(iii)	2122	127	2249	2811	10
1931–32 (i)	1484	26	1510	1888	7
(ii)	1539	13	1552	1940	7

spite, however, of this great number of midges on the wing in 1929, the damage done that year was only about 7 per cent. As these calculations are based on the numbers of insects emerging the following year and not direct larval counts, it is apparent that whatever mortality was due to climatic or biotic factors during the winter is completely masked. In this case, for instance, the progeny of the large numbers of midges on the wing in 1929 may have done a very large amount of damage, and then a harmful winter (1929–30) may have prevented the majority of these larvae emerging as adults in the summer of 1930. Incidentally the winter 1929–30 was, at Harpenden, milder than the previous one. This method of estimating the crop damage of the previous year by emergence figures of the subsequent year rather than direct larval counts is therefore untrustworthy. The emergence method, however, should give a comparative indication of what damage is to be expected in the coming season, provided of course the midges and parasites that emerge oviposit successfully and the resulting larvae feed successfully. It must be remembered that, owing to the conditions being limited under which oviposition can be carried out successfully, changes in the weather about this period are extremely important. We can test how this hypothesis works in practice roughly by comparing the figures of emergences obtained in 1929–32 for the wheat blossom midges with the damage done as estimated by direct larval counts. Table II sets this forth. There is an absence of correlation between the numbers of midges emerging and the extent of subsequent damage, e.g. the same amount of crop damage followed the emergence of 181 midges in 1929 and 1697 midges in 1930. It has been said a rough test can be made

of this hypothesis advisedly, because it has always been observed that a very much lower percentage emergence is obtained when dealing with a species whose larvae go to the soil for the winter than is the case when dealing with larvae which remain in the seed case or gall. For example, 75–84 per cent. of *D. alopecuri* emerged compared with only 15–17 per cent. of *Contarinia merceri*, a soil wintering form (**1**). This may be a natural occurrence or it may be due to error in breeding technique.

Table II. *Numbers of midges emerging and the subsequent crop damage as found by direct larval counts.*

Year	Number of *C. tritici* emerged	% crop damage	Number of *S. mosellana* emerged	% crop damage
1929	181	5·9	47	1·8
1930	1697	5·8	83	11·7
1931	873	6·4	88	15·0
1932	1905	4·9	110	10·5

It will be seen therefore that estimating forthcoming damage by the emergence method is attended by too many restrictions to be really feasible in practice.

V. Degree of relative parasitism of the midge.

(i) *Identification.*

Owing to the courtesy of Sir Guy Marshall, Dr Ferriére of the Imperial Institute of Entomology has identified some of the parasites. There are two species of Chalcids both belonging to the Tetrastichini, viz. *Aprostocetus caudatus* Westwood and *Tetrastichus roesellae* Nees. In addition there is one Proctotrypid Platygasterine, viz. *Prosactogaster attenuata* Hal. *T. roesellae* Nees. has been reared previously by the writer from *Dasyneura leguminicola* Lintn. Dr Ferriére tells me that all three species are supposedly primary parasites. It is hoped at a future date to go through all the tubes of parasites and find out how prevalent each species was during the five years they were under observation.

(ii) *Methods and results.*

The same methods as were used in the previous study on the wheat blossom midges have been applied in this case. Briefly, the infested grass heads have been put into rearing cages and, by finding the proportion of parasites emerging the subsequent year to the number of midges, a figure for relative or effective parasitism has been obtained. This is the number of parasites on the wing compared with the number of midges which will be causing the season's infestation or damage.

Table III shows the results obtained. In locality A it will be observed that there has been marked fluctuations in the extent of parasitism which has varied from 38 per cent. to just over 2 per cent., while in locality B there

have been fluctuations but not of the same magnitude. Further, whereas in locality A the parasitism went up in 1930 (2·3 to 19) in B it went down (2·7 to 0·7). But in 1931 it went up and in 1932 it went down in both localities.

A suggested explanation for the sudden drop in parasitism from 38 per cent. to just over 2 per cent. is given in the next section dealing with emergence.

Table III. *Relative parasitism figures, obtained by breeding in the insectary, of* D. alopecuri *in* 1928–32 *in two localities* (*A and B*) *near Aberdeen.*

Year	Date of sample	Samples of relative parasitism			Average
Locality A					
1928	27. vii. 27	38	—	—	38
1929	9. viii. 28	2·3	—	—	2·3*
1930	26. vii. 29	19	—	—	19
1931	30. vii. 30	31	22	—	26·5
1932	24. vii. 31	2·9	3·1	—	3
Locality B					
1929	23. vii. 28	2·9	2·5	—	2·7
1930	10. viii. 29	0·6	1·1	0·5	0·7
1931	30. vii. 30	3·8	5·7	5·6	5·3
1932	24. vii. 31	1·7	0·8	—	1·3

* This low figure is supported by similar ones obtained from samples which emerged during the winter and summer under different experimental conditions of temperature.

VI. Emergence.

Some factors which affect the emergence of this midge have previously received some attention (**2**). It appears probable that favourable weather in May will cause emergence to start and that such emergences are closely correlated with day-to-day temperatures. On the other hand, after a certain date emergence will proceed very rapidly and the day-to-day temperatures will have less effect on the numbers.

Further, daily fluctuations in numbers emerging were shown in some cases to be very marked as regards the relative numbers of the sexes; one day perhaps would show an almost complete lack of females, another day practically only males, other days would show a marked decrease in both sexes. It was found that the factors affecting daily emergence numbers apparently do not exert their influence on both sexes to the same degree and also that such effects were not lethal but only delayed emergence.

The effects of light and temperature were also studied. The light was shown to affect the time of day of emergence and the females were more affected than the males. If the larvae were subjected to warm temperatures emergence could be made to take place throughout the winter. The effect of cold appeared to be very slight, but further experiments are still required to confirm this.

Table IV shows the dates of the actual first emergence and the peak of emergence of *D. alopecuri* in 1928–32. It must be remembered that these samples were kept in an outdoor insectary at Rothamsted from July or August immediately after gathering until emergence was completed the following

year. It will be seen at once that the range of first emergences is from May 9th to 27th (18 days), while that of the peaks is from May 26th to June 14th (19 days). Even in the same year the different samples have shown (1930) almost the same range in date of first emergence. The peak also varies considerably within the samples of some years (e.g. 1930 and 1932). Similarly the time that elapses between the first emergence and the peak varies from 8 to 33 days (from 11 to 22 days in 1930, and 8 to 15 days in 1929).

Table IV. *Dates of actual first emergence and at peak of emergence of* D. alopecuri, 1928–32.

Year	Date of first emergence	Date of peak of emergence	Days to reach the peak
1928	May 13	June 14	33
1929 (i)	„ 21	„ 4	15
(ii)	„ 26	„ 2	8
(iii)	„ 26	„ 7	13
1930 (i)	„ 12	„ 2	22
(ii)	„ 27	„ 6	11
(iii)	„ 20	May 30	11
(iv)	„ 13	„ 30	18
1931 (i)	„ 12	„ 26	15
(ii)	„ 13	„ 27	15
(iii)	„ 9	„ 27	19
(iv)	„ 16	„ 29	14
(v)	„ 19	„ 28	10
1932 (i)	„ 17	June 2	17
(ii)	„ 20	„ 5	17
(iii)	„ 23	„ 13	22
(iv)	„ 23	„ 12	21

It is obvious that too much reliance cannot be placed on the exact dates since there is so much variation between the different samples of any given year, in spite of the fact that the samples were all kept within a yard and a half of each other in the insectary and so under the same conditions.

The dates and figures in Table V show the weekly emergences of the midge and its parasites. The top rows of figures in each case refer to the midges, while the lower rows refer to the parasites. The peaks are italicised. It will be seen that a crest of emergence has occurred once only in the week May 21st to 27th, nine times in the week May 28th to June 3rd, four times in the week June 4th to 10th and three times in the week June 11th to 17th. Yet there is considerable variation between the different samples even in the same year, e.g. 1931 and 1932.

The emergence of the parasites also varies; once the peak occurred in the week June 4th to 10th, six times in the week June 11th to 17th, nine times in the week June 18th to 24th, and once in the week June 25th to July 1st. It is apparent that in the aggregate the crest in emergence of parasites occurs in the third week after that of the host midge. (This interval varies from 1 week to 3 weeks.) This allows sufficient time for the egg and larvae of the midge to reach the stage of development optimal for parasitisation.

Table V. *Weekly emergence of* D. alopecuri *and its parasites*, 1928–32.

The upper rows of figures refer to the midges, while the lower refer to the parasites. The peaks are italicised. Asterisks mark the two halves of one sample.

Year	Size of sample (heads of grass)	May 7–13	May 14–20	May 21–27	May 28–June 3	June 4–10	June 11–17	June 18–24	June 25–July 1	July 2–8	July 9–15	July 16–22	Later	Total host and parasites	Parasitism %
1928	106	2	1	3	187	350	*708*	196	110	18	13	.	.	1588	38
		.	.	.	27	*337*	274	146	144	34	13	3	1	979	
1929	84*	.	.	161	*3716*	3255	422	329	12	2	.	.	.	7897	2·9
		.	.	18	4	4	69	*94*	44	7	1	.	.	241	
,,	84*	.	.	48	*2248*	2175	183	154	5	.	.	.	.	4813	2·5
		.	.	10	5	2	*46*	35	16	7	1	.	.	122	
,,	50	.	.	6	553	*1276*	179	337	15	5	1	2	.	2374	2·3
		.	.	1	1	0	6	*17*	15	15	2	.	.	57	
1930	91	2	23	241	*568*	347	59	3	1	.	.	.	.	1244	19
		.	.	.	1	15	64	*145*	54	4	1	.	.	284	
,,	105	.	.	1	321	*1533*	693	106	5	3	.	.	.	2667	0·6
		.	.	.	.	.	6	*10*	1	.	.	.	.	17	
,,	105	.	1	80	*643*	354	64	2	.	.	.	.	.	1154	1·1
		.	.	.	.	2	7	4	.	.	.	.	.	13	
,,	100	.	38	229	*514*	92	12	.	.	.	.	.	.	885	0·5
		.	.	1	0	0	1	2	.	.	.	.	.	4	
1931	100	3	40	*980*	560	251	36	19	3	.	.	.	.	1892	3·8
		.	.	.	.	9	*38*	19	7	1	.	.	.	74	
,,	100	4	11	412	705	*752*	95	27	10	.	.	.	.	2016	5·7
		.	.	.	2	11	*55*	43	10	.	.	.	.	121	
,,	100	4	22	773	*996*	287	14	16	10	.	.	.	.	2122	5·6
		.	.	.	1	21	*46*	39	17	3	.	.	.	127	
,,	100	.	2	92	*413*	197	13	8	2	.	.	.	.	727	31
		.	1	2	0	12	138	*141*	30	2	2	.	.	328	
,,	100	.	2	111	*695*	351	27	12	4	.	.	.	.	1202	22
		.	.	1	6	15	*154*	118	41	4	.	.	.	339	
1932	100	.	8	106	*594*	569	168	37	1	1	.	.	.	1484	1·7
		.	.	.	.	.	2	*15*	9	.	.	.	.	26	
,,	100	.	2	53	*475*	*709*	262	37	1	.	.	.	.	1539	0·8
		.	.	.	.	.	1	*9*	2	1	.	.	.	13	
,,	100	.	.	12	147	337	*519*	57	4	.	.	.	.	1076	2·9
		.	1	2	5	1	4	*12*	4	4	.	.	.	33	
,,	100	.	.	3	144	411	*714*	80	3	.	.	.	.	1355	3·1
		.	.	2	9	1	9	9	*12*	1	.	.	.	43	

In one year, however, the crest of parasites actually occurred in the week before that of the midges, viz. in 1928. We have not sufficient data to explain this, but some factor or factors may have retarded the development of the midges, while hastening that of the parasites. This alteration in relative times of emergence of host and parasites is very striking and may be a possible explanation of the very great increase of midges and lowering of the relative parasitism in the subsequent year, already referred to in sections IV and V (ii) of this paper. But a similar fall in parasitism occurred in 1932 in locality A (see Table III) when the relative periods of emergence of host and parasites had been apparently quite normal the previous year.

The greatest value of ascertaining the dates of emergence at present lies in the fact that it enables one to fix the date before which the grass must not be allowed to flower if a control is required (1). It is hoped to make a subsidiary study of the climatic conditions and try to find out whether there are correlations between emergence and any such factor. This would however appear difficult, as there is so much variation between different samples kept under identical conditions. If experiments under controlled conditions were to be set up they should indicate how the insect reacts to certain limited and specified conditions, but would we be any nearer to prediction than we are at present?

VII. Sex ratio of *D. alopecuri* (Reuter).

In a previous paper (3) it was shown that the sexes at emergence were about equal in numbers. Occasionally there was a marked diminution in the numbers of one sex, e.g. a sample from Shropshire gave a ratio of 25:75. It is proposed now to give additional figures obtained from the two Aberdeen localities during the last five years. No significant variation is shown although there is a tendency for females to be in excess.

Year	Males	Females	Sex ratio
	Locality A.		
1928	806	782	51 : 49
1929 (i)	3607	4290	46 : 54
(ii)	2296	2517	48 : 52
1930	607	637	49 : 51
1931 (i)	411	316	57 : 43
(ii)	525	677	44 : 56
1932 (i)	662	822	45 : 55
(ii)	684	855	44 : 56
	Locality B.		
1929	966	1408	41 : 59
1930 (i)	1236	1431	46 : 54
(ii)	498	656	43 : 57
(iii)	405	480	46 : 54
1931 (i)	709	1183	38 : 62
(ii)	795	1221	39 : 61
(iii)	1084	1038	51 : 49
1932 (i)	416	660	39 : 61
(ii)	602	753	44 : 56

VIII. Summary.

1. This is the second of a series of papers in which the fluctuations of insect populations in the field are being studied.

2. The degree of infestation or intensity of attack by the larvae, the degree of parasitism and the dates of emergence (host insect and its parasites) of *Dasyneura alopecuri* (Reuter), which prevents seed production in Meadow Foxtail grass, have received attention over a period of five years. The methods used have been fully discussed.

3. It would appear possible that reversal in the relative times of emergence of host and parasites may account for sudden changes in the degree of parasitism and, subsequently, changes in the extent of damage suffered by the crop.

4. It is desired to hold over a complete discussion of the results until similar studies on other species of gall midges have been completed.

IX. Acknowledgments.

I should like to thank Dr Guy Morison for supplying me with the samples of grass throughout the period of this study, Dr Ferriére who has identified the parasites, and also Dr A. D. Imms and Dr C. B. Williams who have helped me considerably by discussing the work from time to time.

References.

(1) **Barnes, H. F. (1930).** "On the biology of the gall-midges (Cecidomyidae) attacking Meadow Foxtail Grass (*Alopecurus pratensis*), including the description of one new species." Ann. App. Biol. 17, 339–66.

(2) **Barnes, H. F. (1930).** "On some factors governing the emergence of gall midges (Cecidomyidae, Diptera)." Proc. Zool. Soc. Lond. 381–93.

(3) **Barnes, H. F. (1931).** "The sex ratio at the time of emergence and the occurrence of unisexual families in the gall midges (Cecidomyidae, Diptera)." J. Genetics, 24, 225–34.

(4) **Barnes, H. F. (1932).** "Studies of fluctuations in insect populations. I. The infestation of Broadbalk wheat by the wheat blossom midges (Cecidomyidae)." J. Animal Ecology, 1, 12–31.

(5) **Barnes, H. F. (1932).** "A study of the segmentation of the antennae in gall midges (Cecidomyidae)." Proc. Zool. Soc. Lond. 323–34.

(6) **Barnes, H. F. (1932).** "Periodic fluctuations in the prevalence of the wheat blossom midges." J. Animal Ecology, 1, 191–2.

THE MICE OF ST KILDA, WITH ESPECIAL REFERENCE TO THEIR PROSPECTS OF EXTINCTION AND PRESENT STATUS

By T. H. HARRISSON and J. A. MOY-THOMAS.

(*With Plate IV.*)

I. Introduction.

The island group of St Kilda, 50 miles west of the Outer Hebrides, was evacuated of all inhabitants and nearly all sheep in September, 1930. In July and August, 1931, a party of six visited the islands in order to examine the effects of depopulation and cessation of grazing on the fauna and flora. Owing to the difficulty of reaching the smaller islands, trapping was confined to the main island of Hirta, the only one that had been inhabited, and to which six of the inhabitants returned for the summer months of 1931. Since the following observations were made the position has been complicated by several islanders being permitted to return in the summer of 1932.

The authors are indebted to Sir Guy Marshall, F.R.S., of the Imperial Institute of Entomology for the identification of the fleas, and to Dr S. Finnegan of the British Museum (Natural History) for identifying the mites.

II. The house mouse of St Kilda, *Mus musculus muralis* Barrett-Hamilton.

(*a*) *Previous history.*

The house mouse of St Kilda was first noted by Seton in 1878 (**13**), but was first collected in 1894 by Steele Elliot (**14**, **15**) who noted its difference from ordinary house mice. In 1899 Barrett-Hamilton described it as a new form, *Mus muralis* (**1**, **2**). Waterston in 1905 (**17**) remarked on the abundance of *Mus muralis*, which "swarms in all the cleits and houses within the cultivated area." He also stated that it is very prolific and omnivorous. Eagle Clarke in the same year (**6**) noted that house mice captured in Lochmaddy, North Uist, by Waterston in every way resembled the light-bellied *Mus muralis*, being found living with the normal *Mus musculus*, but apparently without hybrids. Barrett-Hamilton (**4**) examined specimens collected by Waterston on St Kilda and was confirmed in the view that *Mus muralis*, like *Mus musculus faroensis*, was a robust development from *Mus musculus*. Trouessart in 1910 (**16**), in his "Faune Mammifère d'Europe," designated *Mus muralis* a subspecies, *Mus musculus muralis*. Eagle Clarke (**7**) trapped about forty specimens in 1910 and 1911, and took measurements of 29 specimens whose head and body exceeded 90 mm. in length. He remarked that

they were very common and not confined to the houses, but occurred in the crofts, sheltering in the walls and loose stone buildings or cleits. Ritchie (**12**), describing the fauna of St Kilda, remarked that "*Mus muralis*...is confined to the Post Office buildings," an error into which Macgregor (**11**) also falls (see below).

Apart from published accounts of the mice the six native St Kildans who returned in 1931 stated that the mice were abundant in all the inhabited houses up to the evacuation in 1930, and that house No. 16 had always been very much overrun with mice, but that mice had never been recorded in the Post Office itself, a fact which seemed likely owing to the complete absence of holes.

(*b*) *Methods.*

Our object was to take a census without reducing the mouse population. The traps used were either wooden "lever" ones of the "alive" type, or of the weight-release type of metal trap, kindly supplied by C. S. Elton and A. D. Middleton of the Oxford Rodent Investigation. The baits (coconut, cheese, and bacon) were constantly varied, no preference for any particular bait being found.

The mice were marked, so that individuals could be distinguished. Measurements of living mice were impracticable, but weights were taken in all cases, a spring balance being used. In the four cases where mice were either found dead in the traps or were killed, full measurements were also taken, the skins and skulls preserved, and the stomach contents examined.

(*c*) *Trapping results.*

Every house and cleit was trapped with six traps for six days during late July and early August, 1931, the position of most traps being changed daily. Where results were obtained, the number was increased to ten traps in each room. In the other houses and cleits the number was reduced by half, and the remaining traps left for a further six days, and finally removed.

The houses consist of two main rooms, and one very small room. Traps were set in all rooms, and in the lofts. The houses were numbered by the inhabitants from 1 to 16, and it was found that only numbers 8 (one mouse only) and 16 contained any mice. A greater number of traps were set also in the Manse and Factor's house with negative results. In No. 16, however, mice were comparatively abundant, and ten different mice were identified by means of marking. Of the mice caught five were males and six were females of the following weights:

Males: 24, 24, 26, 28, 32 gm.

Females: 18, 19, 22, 24, 24, 32 (No. 8) gm.

Three of these had died in traps and were measured:

Male: 32 gm., head and body 96 mm., tail 93 mm., ear 13 mm., hind-foot

19 mm. *Male:* 26 gm., measurements as before, 92, 86, 15, 19 mm. *Female:* 18 gm., measurements as before, 85, 85, 13, 17 mm.

An interesting fact was the frequency of return to the traps of certain individuals, some mice being caught as often as twice in the same day, and some every day for a week. There seemed very little difference between the number caught in the daytime and the number caught at night.

The only other house mouse caught was trapped on the outside of a cleit near the churchyard, an area where field mice were abundant. This mouse, a young male, weighed 20 gm., and measurements 81, 76, 12, 18 mm. Lines of from thirty to forty traps were set nightly round the cleits and fields adjoining the houses, but only field mice were caught.

It was clear that the presence of house mice in these two houses only, was due to the fact that a certain amount of food still remained in them (flour, dried fish, and sugar). The total house mouse population of Hirta in August, 1931, was probably not less than twelve, but cannot have been much more than twelve. Twenty-five would be a very liberal estimate indeed.

The female killed contained no embryos, and none of the other mice captured appeared to be in breeding condition. It seems doubtful if more than one young mouse was present. Food scarcity may well have caused this. The stomach contents of those mice killed revealed nothing definite about their food. Two external parasites were found on the house mouse, a flea, *Ceratophyllus fasciatus* Bosc., and a mite, *Eulaelaps stabularis* C. L. Koch. Both are not uncommon parasites on small rodents, *Ceratophyllus fasciatus* being a typical flea of house mice and rats, and sometimes occurring on wild mice.

(*d*) *Future of the St Kilda house mouse.*

It is clear that the house mouse must be much rarer now than it was when the island was inhabited. The two chief factors which affected the numbers during 1931 were the food supply and cats. The supply of artificial food is now greatly diminished, and unless the mouse can live on some other kind of food extinction seems almost inevitable. It is frequently stated that mice go out into the fields during the summer, returning to the houses during the winter. Except for the fact that a single mouse was trapped in the arable area by the churchyard, there is little evidence that they go out during the summer on St Kilda, because during extensive trapping all round the village no other house mouse was caught.

According to the inhabitants, about a dozen cats had been left in 1930. In July, 1931, there appeared to be only three left. Two females, one with kittens, were shot, but a third escaped. The cats were not only destroyed on account of the mice but also on account of the St Kilda wrens and other small birds which form a part of their diet. The cat factor has now been mainly removed and the future of the house mouse is one of food. Will the mouse take to fields or will it become extinct through lack of nourishment?

It is by no means an unknown event for a house mouse to become wild again, as in the case described by Jameson (**10**) from North Bull, Dublin Bay, Ireland, and also in many parts of North America. We, however, found practically no evidence of this, and it must therefore be concluded that *Mus musculus muralis* is doomed to become extinct on Hirta.

III. The long-tailed field mouse of St Kilda, *Apodemus* (*Mus*) *sylvaticus hirtensis* Barrett-Hamilton.

(*a*) *Previous history.*

This mouse was described as a new species, *Mus hirtensis*, by Barrett-Hamilton in 1899 (**1**), having the same characters as *Mus hebridensis* but differing in size and colour. In 1900 (**3**) Barrett-Hamilton reduced it to a subspecies, *Mus sylvaticus hirtensis*. Waterston (**17**) gave a very complete account of the nest, habits, habitats, and internal parasites of the mice, all of which we were able to confirm, except the record by an islander of a mouse from the top of Conachair (1396 ft.). We captured no mouse above 550 ft. and none in the very short grass characteristic of the top of Conachair. Waterston's collection of mice was examined by Barrett-Hamilton, and he emphasised the variation in colour. Eagle Clarke (**7**) collected sixty mice in 1910 and 1911, and took measurements of forty-two, whose head and body measured more than 100 mm. He modified the description of the animal, which stated that an important character of the species was that the underside was heavily washed with yellowish brown; he noted that in the majority of the adults and in many of the immature ones the throat, chest, and abdomen are white.

Waterston observed that the sex ratio of mice caught was 2:1, the males outnumbering the females, and Eagle Clarke found that the sex ratio of mice caught was approximately equal. The authors found that the males outnumbered the females by about 3:1 of all individuals trapped; these figures include mice caught more than once, and are therefore not strictly comparable with the foregoing figures.

(*b*) *Methods.*

One of the objects of the visit was to obtain a trap census of the field mice to give future observers figures representing the numbers in the different environments. Traps were set out in rows of about fifty at about five yards' interval, (*a*) in different habitats, (*b*) at varying heights of approximately 50 ft. The traps used were of the lever "alive" type used as in the houses, except where they were impractical in crevices on stone walls. Every precaution was taken to kill a minimum of specimens, in order to leave them in as natural a state as possible. The only bait used was coconut. The weather conditions were noted each night and were found to make an appreciable

Phot. 1. A typical "cleit" or loose stone building, from the arable land in front of village.

Phot. 2. General view of Village Bay, showing houses, Conachair in background, and arable land in foreground.

difference to the number of mice caught. Each line of traps was left for about ten days.

Trapping was only carried out on Hirta, although mice have been recorded from Dùn and Soay as well. On Dùn, where the grass is long, mice runs were commonly seen, but in the single visits made to Soay and Boreray no runs were noticed.

(c) *Trapping results.*

A typical line of fifty traps set in the village area with many cleits and long grass between July 24th and August 5th gave the following nightly numbers of mice: 5, 3, 4, *0*, 5, 5, 4, 3, 4, *1*, 5, 4, 4 (the figures in italics were for wet, stormy nights). From figures such as these, nightly averages were obtained for fifty traps, excluding abnormal nights when it rained most of the night, the average for the example just given being about four mice per night[1].

The island was divided up into three types of area for trapping purposes:

(1) South-east side of the island with many stone walls, buildings, and long grass (Village Bay Area):

(*a*) Cliff and shore area. 0–50 ft. Average for 50 traps per night	2 mice
(*b*) Arable land in front of village. 50–100 ft. Average for 50 traps per night...	3·5 mice
(*c*) Village area. 100–150 ft. Average for 50 traps per night	4 mice
(*d*) Area behind village (arable moorland transition). 150–200 ft. Average for 50 traps per night	2·5 mice
(*e*) Lower slopes of Conachair. 250–300 ft. Average for 50 traps per night ...	1 mouse
(*f*) Slopes of Conachair. 300–350 ft. Average for 50 traps per night	0·25 mice
(*g*) Slopes of Conachair. 350 ft. upwards. Average for 50 traps per night ...	No mice

(2) North-west side of the island with some long grass at low levels but few buildings:

(*a*) Up to 200 ft. Average for 50 traps per night ...	2·5 mice
(*b*) 200–300 ft. „ „ ...	1 mouse
(*c*) 300–400 ft. „ „ ...	1·5 mice
(*d*) 400–500 ft. „ „ ...	0·75 mice
(*e*) 500 ft. upwards. „ „ ...	Only 1 mouse at 550 ft.

(3) Short-cropped area above 300–400 ft. of the moorland type with *Festuca ovina*, *Nardus stricta*, and always traces of *Calluna vulgaris*. At all heights mice were very scarce, an exceptionally good average catch being 0·1 mice per 50 traps per night.

Most of the trapping was done at (1) where the species was generally distributed in the vicinity of stone walls, cleits, and houses at low levels, being especially numerous around the village graveyard. At (2) it was confined to similar localities which were far less numerous. Elsewhere mice were practically absent, despite the presence of numerous cleits all over the hillsides.

Mice may thus be said to occur commonly in the arable and transitional

[1] It should be remembered that these trapping figures include individuals caught more than once and are not comparable to a trap census in which the mice are killed.

arable moorland habitats of lower levels, *so long as there are walls or buildings in the vicinity*; but that elsewhere they are scarce or absent. Mice are said to occur on all the smaller islands—Soay, Boreray and Dùn. They are certainly quite exceptionally abundant on an area of *Cochlearia anglica* and *Atriplex babingtonii* adjacent to a cave high up on the north side of Dùn, which is an island ecologically composed entirely of moderately sloping sea-cliff. Whether mice occur generally in this habitat we were unable to ascertain, owing to the difficulty of trapping or even of reaching many such areas which constitute a large part of the cliffs for which St Kilda is justly famous.

All the mice were weighed. Owing to the large number of mice captured only the percentage weights are given: *Males:* 40 per cent. 14–20 gm., 36 per cent. 21–30 gm. and 24 per cent. 31–50 gm. *Females:* 31 per cent. 15–20 gm., 26 per cent. 21–30 gm. and 43 per cent. 31–42 gm.

Grass forms the staple diet—*Holcus lanatus*, *Anthoxanthum*, *Festuca ovina*—and in addition seeds of *Cochlearia anglica*, *Statice maritima*, *Ranunculus acris*, *Rumex acetosa* were recorded.

In the few animals killed, Cestode parasites were observed. Waterston (**18**) had previously identified certain Cestode parasites: *Cysticercus fasciolaris* Rud. (the larvae of *Taenia crassicolis* Rud.). The Coccidia noted by Waterston (**18**) were not observed. Two ectoparasitic mites, *Laelaps festinus* C. L. Koch, and *Eulaelaps stabularis* C. L. Koch, were identified; both are recorded from *Apodemus sylvaticus* in Bagley Wood, Oxfordshire (**8**).

IV. Summary and conclusions.

After intensive trapping inside all the houses, and further trapping round the village and all over the island, it was discovered that only two houses still contained St Kilda house mice. The general absence of any house mice in the outside traps made it almost certain that since the evacuation of the islanders in September, 1930, *Mus musculus muralis* has greatly decreased in numbers, and in July, 1931, was rapidly dying out through lack of food. It is very unlikely that there were more than twenty-five individuals in August, 1931, on St Kilda, though the evidence of Waterston's mice raises the question of its occurrence on other islands in the Outer Hebrides, an important possibility which has not been investigated (**9**).

A trap census of the St Kilda field mouse revealed that the animal was fairly numerous over most of the island below 400 ft. The mouse was only very rarely caught in short grass or moorland, but was common in long grass areas of *Holcus lanatus*, *Anthoxanthum*, etc. and was found to be abundant where there was any stone wall or cleit at low level. The mouse was found to be entirely nocturnal, never being noted or trapped during the day. The sex ratio of total animals trapped was found to be about 3 males to 1 female, and a very large percentage of juveniles was caught. It was impossible to

compare the numbers with those before the evacuation as no figures have ever previously been recorded, but the abundance of mice in the village area is possibly a new development since evacuation.

The species of field mouse therefore continues to thrive. The evacuation may have important indirect effects, for the removal of the sheep will lead to a development of *Calluna*, which will become dominant over much of the island. The present mouse habitats may be threatened to a considerable degree; at present however the species is unaffected, but a careful investigation some years hence will prove essential.

REFERENCES.

(1) **Barrett-Hamilton, G. H. (1899).** Proc. Zool. Soc. 77–88.
(2) **Barrett-Hamilton, G. H. (1899).** Ann. Scott. Nat. Hist. 129–40.
(3) **Barrett-Hamilton, G. H. (1900).** Proc. Zool. Soc. 397–428.
(4) **Barrett-Hamilton, G. H. (1906).** Ann. Scott. Nat. Hist. 1–4.
(5) **Barrett-Hamilton, G. H. (1910).** "History of British Mammals." London.
(6) **Eagle Clarke, W. (1905).** Ann. Scott. Nat. Hist. 198–9.
(7) **Eagle Clarke, W. (1914).** Scott. Nat. 124–8.
(8) **Elton, C., Ford, E. B., Baker, J. R.** and **Gardner, A. D. (1931).** Proc. Zool. Soc. 657–721.
(9) **Harrisson, T. H.** and **Moy-Thomas, J. A. (1932).** Nature, Jan. 23.
(10) **Jameson, H. L. (1897).** J. Linn. Soc. 26, 465–73.
(11) **Macgregor, A. A. (1930).** "A last voyage to St Kilda." London.
(12) **Ritchie, J. (1930).** Scott. Nat. 69–74.
(13) **Seton, J. (1878).** "St Kilda past and present." London.
(14) **Steele Elliot, J. (1895).** J. Birm. Nat. Hist. Soc. 135.
(15) **Steele Elliot, J. (1895).** Zoologist, 281 and 426.
(16) **Trouessart, E. L. (1910).** "Faune Mammifère d'Europe." Berlin.
(17) **Waterston, J. (1905).** Ann. Scott. Nat. Hist. 199–202.
(18) **Waterston, J. (1906).** Ann. Scott. Nat. Hist. 150–3.

NOTES

NUMBERS OF GANNETS (SULA BASSANA) IN SCOTTISH ISLANDS.

J. H. GURNEY gave estimates of numbers in each gannetry prior to 1913 in his book *The Gannet*; since that time some additional and more accurate data have been obtained. In 1914 the Duchess of Bedford (*Scottish Nat.*, 1914, 176) estimated 5000 birds on the Stack of Stack and Skerry: this is 3000 less than Gurney's figure. In 1929, J. Bain (see J. Ritchie, *Scottish Nat.*, 1929, 127) made a detailed count of the Bass Rock Colony and found 8294 birds, considerably more than Gurney. In July, 1931, I found 21,300 adults on St Kilda, of which 16,000 were on Stac Lee, 7000 on Stac an Armin, and 4300 on Boreray in four groups (including Creagan na Rubhaig 1800, and Clagan na Ruskachan 1100). Gurney estimated 30,000 on data supplied by the very unreliable natives to Wingfield-Worth (*St Kilda and its birds*, 1903), their Boreray information being unsound. In August, 1931, I made a rough long-distance estimate of 9000 adults on Suilsgeir, concentrated on the south and south-east cliffs. This is 1000 more than Gurney's figure, based on Harvie Brown's 1887 visit (*Proc. Roy. Phys. Soc. Edinburgh*, 1885–6, 290).

Allowing for Gurney's bad estimates there has been a considerable increase in the last thirty years and at least six new colonies have recently been formed in the Shetlands, Forth and Wexford. This increase and spread shows every sign of being correlated with the depopulation of small Scottish islands and the increase in the use of tinned foods, etc. by the islanders. I hope shortly to study the spread, increase and consequent repercussions in detail, and shall be glad of data on the subject, c/o the Editor of this *Journal*.

T. H. HARRISSON.

THE SWALLOW MORTALITY IN CENTRAL EUROPE IN SEPTEMBER, 1931.

During the second half of September, 1931, a cyclone over Poland produced a sudden cold spell in southern Germany, Austria and Hungary. Snow fell on the mountains and steady cold rain fell in the Danube valley. Immense numbers of swallows and house martins, and some sand martins, numbed by the cold and unable to find food, sought shelter in stables, barns and houses, where, in some cases, they congregated in great masses and were so inert that they could be picked up by hand. In Austria the public were invited to send them in to the Vienna Zoological Gardens where they were placed in a warm building and supplied with mealworms. About 80,000 were transported thence by aeroplane and train to Venice, where they were liberated. Of birds collected in Hungary 450 were forwarded by train from Budapest to Constantinople.

Among the birds picked up dead or moribund in the period September 22–30, 21 swallows, 7 house martins and 1 sand martin bore rings issued by the Heligoland or Rossitten bird stations, and the directors of those two stations have published a list[1] giving the details of ringing and recovery from which

the accompanying map has been prepared. Three house martins with Heligoland rings found at Budapest have not been included as the numbers on the rings were not read so that it is not known where they were ringed. It will be

[1] **Drost, R. and Rüppell, W. (1932).** "Ueber den Zug deutscher Schwalben in Europa." Der Vogelzug 3, 10–17.

noted that the area in which birds were overwhelmed extended from Basle to Cracow and from Dresden south to Sarajevo, so that the 90,000 individuals rescued at Vienna and Budapest were probably only a small fraction of the total. It will be seen also that the birds affected had all been ringed in Germany, the swallows in an area including Mecklenberg, Prussia, Pomerania, Thuringia, Saxony and Silesia, the house martins in an area including Holstein, Hesse, western Prussia and Saxony, and the single sand martin in western Prussia. The sand martin, the 4 house martins and 18 of the swallows were birds of the year ringed during the summer of 1931; two of the swallows had been ringed in 1930 and one in 1929.

W. B. ALEXANDER.

NOTICES OF PUBLICATIONS ON ANIMAL ECOLOGY

Note. Entomological journals have been abstracted by H. F. Barnes.

1. GENERAL PAPERS ON PARTICULAR GROUPS OF ANIMALS.

1. Pearman, J. V. (1932). "Notes on the genus *Psocus*, with special reference to the British species." Ent. Mo. Mag. 68, 193–204.

2. ECOLOGICAL SURVEYS AND HABITAT NOTES.

(*a*) Marine.

2. Otter, G. W. (1932). "Rock-burrowing echinoids." Biol. Rev. 7, 89–107.

(*b*) Freshwater.

See also **13, 16.**

3. Lowndes, A. G. and **Calman, W. T. (1932).** "Occurrence of *Bathynella* in England." Nature, 130, 61–2.

This minute Anaspid Crustacean was found in the Bath Stone Quarries at Corsham, near Bath. It has previously been found in underground waters in Central Europe, and the only related forms are now confined to Tasmania, Central Europe and the Malay Peninsula.

(*c*) Land.

See also **27.**

4. Edwards, F. W. (1932). "Insects in dead ragwort stems." Entomologist, 65, 166–7.

The following were found: pupae of *Agromyza aeneiventris* with two parasites, the Cnipid *Gronotoma? nigricornis* and the Chalcid *Syntomopus? thoracicus*; a moth, probably a *Depressaria*, and a Braconid attacking it, and a Thysanopteron *Bagnallia* sp. feeding on the remains of the moth larva.

5. Lack, D. (1932). "Further notes on insects from St Kilda in 1931; including the orders Thysanura, Dermaptera, Hemiptera, Trichoptera, Lepidoptera, Coleoptera (Supplement) and Hymenoptera." Ent. Mo. Mag. 68, 137–45.

An account of the insect fauna of St Kilda in 1931, one year after the evacuation of the inhabitants. Other notes on this subject by various writers will be found in the same journal, 67 (1931), 276–9; 68 (1932), 146–50, 262, 262–3, 263–6.

6. Chater, E. H. (1931). "A contribution to the study of the natural control of gorse." Bull. Entom. Res. 22, 225–35.

Gorse is sometimes a serious pest in New Zealand although also used for hedging. An ecological study was carried out in England, and this included a study of insects that cause damage to the plant. The distribution of some of these species was worked out. Biological control of seed production and of seed dispersal is aimed at.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS.

See also **41, 43, 49.**

7. Russell, E. S. (1932). "Conation and perception in animal learning." Biol. Rev. 7, 149–79.

8. Russell, E. S. and **Bull, H. O. (1932).** "A selected bibliography of fish behaviour." J. Conseil Intern. pour l'Explor. de la Mer, 7, 255–83.

A list of over 600 papers arranged both under authors and subjects.

9. Savage, R. E. (1932). "*Phaeocystis* and herring shoals." J. Ecology, 20, 326–40.

The variable movements of herring shoals depend partly upon the distribution of food supplies, and these in turn are partly controlled by wind action affecting drift of plankton. The colonial Flagellate *Phaeocystis* produces large areas of water which have a pungent odour and may be discoloured, and these patches appear to be avoided by herring. The position of the plankton varies and it probably has an important influence on the path of herring movements.

10. Lumby, J. R. (1932). "Current systems of the North Atlantic and the North Sea." J. Ecology, 20, 314–25.

The usual maps showing surface currents in the Atlantic are based on wrong conceptions of the vertical layering of oceanic waters. Modifications of older conceptions are clearly described with maps.

11. Himmer, von H. (1932). "Die Temperaturverhältnisse bei den Sozialen Hymenopteren." Biol. Rev. 7, 224–53.

Temperature regulation of nests is well-marked not only in hive bees, where it is best developed, but also in certain social wasps and ants, although in the latter the internal nest temperature fluctuates greatly. This paper contains a full account of work on the subject, in German, with an English summary.

12. Munro Fox, H. and **Simmonds, B. G. (1932).** "Metabolic rate and habitat." Nature, 130, 277–8.

The metabolic rates of the fresh-water Crustacea *Gammarus pulex* and *Asellus aquaticus* are much greater than those of the marine *G. locusta* and *marinus* and *Idotea neglecta*; that of a stream-living mayfly was found to be higher than that of a pond-living form. Similar differences were found in stream and pond caddis larvae, and between individuals of *Asellus* from these two habitats.

13. Southern, R. and **Gardiner, A. C. (1932).** "Reports from the Limnological Laboratory. 2. The Diurnal migrations of the Crustacea of the plankton in Lough Derg." Proc. Roy. Irish Acad. 40, B, 121–59.

An important critique of the methods of studying vertical plankton movements, with special reference to *Daphnia longispina*, *Bythotrephes longimanus*, *Leptodora kindtii*, *Diaptomus gracilis*, *Eurytemora velox*, and *Cyclops strenuus*. Observations were carried out continuously for six days, and counts made at different levels. The results showed the general importance of the daylight cycle, but there was much minor variation in behaviour, partly due to age and sex differences, also errors due to technical difficulties.

14. Russell, F. S. (1932). "Behaviour in invertebrates." Nature, 129, 473.

Referring to the paper (**13**) above; points out that different broods of marine Copepods and of *Sagitta* show different types of behaviour during diurnal migrations.

15. Lowndes, A. G. (1932). "Elutriation and some of its applications to biology." Proc. Linn. Soc. London, 1931–2, 11–14.

This method, previously used in mineralogy for separating particles of different sizes, was used to study the swimming powers of small Crustacea.

16. Keilin, D. (1932). "On the water reservoir of a horse-chestnut tree." Parasitology, 24, 280–2.

This water hole was watched for several years, and found to have a fairly constant mosquito fauna, living in highly alkaline water. The observations afford additional proof that certain mosquito larvae are not inhibited by *p*H values of water.

17. Buxton, P. A. (1932). "Terrestrial insects and the humidity of the environment." Biol. Rev. 7, 275–320.

A full summary of methods and ideas.

18. **Buxton, P. A.** (1931). "The measurement and control of atmospheric humidity in relation to entomological problems." Bull. Entom. Res. 22, 431–47.

A full discussion of methods at present available.

19. **Mellanby, K.** (1932). "Effects of temperature and humidity on the metabolism of the fasting bed-bug (*Cimex lectularius*), Hemiptera." Parasitology, 24, 419–28.

An experimental study of the rates of loss of weight, water, and food reserves in a blood-sucking insect kept without food. Both the techniques and the results are interesting. The bugs have a certain power of regulating water loss from the body.

20. **Rivnay, Ezekiel** (1932). "Studies in tropisms of the bed bug, *Cimex lectularius*." Parasitology, 24, 121–36.

Bed bugs are attracted by the heat of the human body, but may be either attracted or repelled by bodies with different smells. "If the host is wet the bug will not be attracted."

21. **Davidson, J.** (1932). "Resistance of the eggs of Collembola to drought conditions." Nature, 129, 867.

Refers to *Smynthurus viridis* in southern Australia, where hatching of eggs is controlled by moisture.

22. **Cameron, A. E.** (1932). "The rearing of *Haematopota pluvialis*, Linné (Cleg, Tabanidae) under controlled experimental conditions." Nature, 130, 94–5.

23. **Tate, P.** and **Vincent, M.** (1932). "Influence of light on the gorging of *Culex pipiens*." Nature, 130, 366–7.

This mosquito will not feed when kept in the dark, but will do so after prolonged exposure to daylight.

4. PARASITES OF ANIMALS.

See also **4**.

24. **Jones, H. P.** (1932). "*Lipoptera cervi* L. (Diptera: Hippoboscidae) in Nottinghamshire." Ent. Mo. Mag. 68, 233.

Found commonly as parasite on red and fallow deer.

25. **Bristowe, W. S.** (1932). "*Mantispa*, a spider parasite." Ent. Mo. Mag. 68, 222–4.

A summary of the present state of knowledge, with references.

26. **Fraser, J. H.** (1932). "Occurrence of the Cyclopoid, *Herrmannella rostrata* Canu, in *Cardium edule*." Nature, 130, 1932.

27. **Harper, W. F.** (1932). "On some British larval Trematodes from terrestrial hosts." Parasitology, 24, 307–17.

Molluscs in the Dundee and Arbroath districts of Scotland were examined extensively. Five species of larval flukes are described, from the following land snails: *Helix hortensis*, *Polita alliaria*, *P. nitidula*, *P. lucida* and *Lauria cylindracea*.

5. PLANT-GALLS.

28. **Bagnall, R. S.** and **Heslop Harrison, J. W.** (1932). "A preliminary account of the Scottish gall-midges." Scottish Nat. 109–21.

Lists of species with host plants, localities, dates, and some descriptions of the appearance of the larvae.

29. Niblett, M., Burkill, H. J. and **Ross, J. (1932).** "Gall-causing Cnipidae in Britain." Entomologist, 65, 193–7, 232–5, 254–8 and 274–5.

Supplement to paper referred to in *J.A.E.* Notice 42, 1932.

6. FOOD-HABITS.

See also **4, 19, 23, 33, 43.**

30. Barnes, H. F. (1932). "A study of the segmentation of the antennae in gall midges (Cecidomyidae)." Proc. Zool. Soc. London, 1932, 323–34.

In some species and genera food affects the size of the adult midges only: in others it affects the size of adult midges and, in addition, the number of antennal segments.

7. THE NUMBERS OF ANIMALS.

31. Harrisson, T. H. (1932). "Resident and migratory birds of North Rona, the remotest Scottish island." Ibis, 2, 441–57.

This small island used to be inhabited, but was abandoned in 1844. There are still about 200 sheep, which live on the grassy land, and aid in the support of a population of about 100 starlings. Sea birds are abundant, while land birds include only rock-pipits, wheatears and meadow-pipits. Approximate counts were made of most species. The absence of all birds of prey (if one excepts gulls) was remarkable. There appears to have been considerable fluctuation both in numbers and species of birds in past years.

32. Wynne-Edwards, V. C. and **Harrisson, T. H. (1932).** "A bird census on Lundy Island (1930)." J. Ecology, 20, 371–9.

Includes a brief general description of the island and (*a*) a census of existing bird population, (*b*) a co-ordination of records for the birds found in former years. The numbers both of individuals and species appear to have varied greatly. Densities per acre for skylark, meadow-pipit and stonechat were 15·5, 3·1 and 30·2 respectively.

33. Robinson, H. W. (1932). "Changes in the distribution of British grey geese." Scottish Nat. 139–42.

Discusses changes in the last two centuries, and among other points, stresses the relation of geese to different kinds of grass used as food. Further papers on the same subject by **G. Beveridge,** 169–71, and **J. Berry,** 173–7.

34. Tucker, B. W. and others **(1932).** "Report of the Oxford Ornithological Society and the Ornithological Section of the Ashmolean Society for 1931." Proc. and Report, Ashmolean Nat. Hist. Soc. of Oxfordshire for 1931. Supplement.

In addition to notes of the usual type on numbers and occurrence, special attention is given to the wheatear, sand martin, house martin, wryneck, stone curlew, redshank, and snipe. In the urban area there were 20 pairs of house martins to the square mile, in a larger rural district about 9 pairs to the square mile. There are also notes on ringing work at bird traps.

35. McWilliam, J. M. (1932). "Census of black-headed gulls nesting in Bute." Scottish Nat. 150.

A nesting colony of about 600 birds was photographed from the top of a cliff, and the birds counted from the photograph.

36. Russell, E. S. (1931). "Some theoretical considerations on the 'over-fishing' problem." J. Conseil Intern. pour l'Explor. de la Mer, 6, 1–20.

Factors controlling the population of commercially exploited fish are the size of fish of different ages, the rate of growth, number on an area, number caught, and the natural sources of mortality (*a*) in small fish, (*b*) in the large fish that are "catchable." The interaction of these factors is discussed, and the difficulty of making rational fishing plans without forecasts of the numbers of young age-classes several years ahead. Methods of obtaining measures of these different factors in the situation are also discussed, in order to estimate how far theoretical conclusions can be actually tested in practice.

37. Whitehead, T., Currie, J. F. and **Davies, W. Maldwyn (1932).** "Virus diseases in relation to commercial seed-potato production, with a study of the aphid population at selected farms." Ann. Appl. Biol. 19, 529–49.

A preliminary study of potato aphid populations, with particular reference to virus disease transmission.

38. Davies, W. Maldwyn (1932). "Ecological studies on aphides infesting the potato crop." Bull. Ent. Res. 23, 535–48.

The intensity of aphid population was estimated and a technique developed to ascertain the movement of aphides within the crop.

39. China, W. E. (1932). "On the occurrence in Surrey of a genus and species of Capsidae (Hemiptera-Heteroptera) new to Britain." Ent. Mo. Mag. 68, 180–3.

A Mediterranean species, *Campylomma nicolasi*, has suddenly appeared in Surrey in large numbers.

40. Frohawk, F. W. (1932). "Local Abundance of *Tortrix viridana*." Entomologist, 65, 210.

41. Stewart MacLagan, D. (1932). "An ecological study of the 'Lucerne flea' (*Smynthurus viridis* Linn.)." Bull. Entom. Res. 23, 101–45 and 151–90.

An important and comprehensive study of a springtail (Collembola) which, although a polyphagous vegetarian, attacks especially Leguminosae, and has become a pest of alfalfa and clovers, both in Britain, and in southern Australia, where it was probably introduced. An elaborate laboratory study of physical factors controlling fecundity and longevity was made, together with experiments on predators (insects and spiders) of possible use in controlling the springtails. The physiological processes such as reproduction and survival showed different optima, and the writer believes that "population increase in a natural environment is seriously handicapped on account of the diverse physiological ensemble of the individual" and questions the possibility of close adaptation existing for a whole organism. Part 2 deals with field studies of populations and the factors (mainly physical ones) correlated with fluctuations in numbers, the construction of a world map showing theoretically possible distribution of the species, and a discussion of means of control.

42. Turk, F. A. (1932). "Swarming of Collembola in England." Nature, 129, 830–1.

Records of local great abundance of different species. A further note by **W. Maldwyn Davies** (Nature, 130, 94, 1932) states that cannibalism is partly responsible for aggregation of Collembola also the tendency for the insects to collect in damp spots.

43. Brady, F. (1932). "Notes on the distribution of *Macoma baltica* (L.) and *Scoloplos armiger* (O. F. Müller)." Proc. Univ. of Durham Phil. Soc. 9, 31–9.

The numbers of molluscs, properties of mud, and salinity and *p*H of the water, were worked out at a number of stations in Budle Bay. The numbers of *Macoma* varied inversely with those of *Scoloplos*, and competition for food is suggested.

44. Munro Fox, H. "Lunar periodicity in reproduction." Nature, 130, 23.

Discusses possible ways (tides, polarised light, length of light period) in which lunar cycles in reproduction might be caused. Concludes that length of light is the most likely cause.

8. MIGRATION AND DISPERSAL.

See also **6, 9, 10, 13, 14, 31, 34, 39.**

45. Lloyd Praeger, R. (1932). "Recent views bearing on the problem of the Irish flora and fauna." Proc. Roy. Irish Acad. 41, B, 125–45.

Mainly a full discussion of the relation of land-bridges to the origin of Irish animals and plants. The writer concludes that accidental dispersal is not enough to account for many of the plants, and more especially of the Irish animals. He believes that they reached Ireland partly after the last glacial maximum, partly in interglacial times.

46. Stephen, A. C. (1932). "Notes on some whales recently stranded on the Scottish coast." Scottish Nat. 163–7.

The following numbers were recorded: three in 1929, none in 1930, four in 1931, and ten in 1932. The last ten belonged to eight species, including one Arctic white whale caught in the Forth River.

47. Russell, F. S. and **Kemp, S. (1932).** "Pelagic animals off the south-west coasts of the British Isles." Nature, 130, 664.

Collected records of the arrival alive in British waters of the Siphonophore *Velella spirans*, which was abundant in 1932, together with the pelagic Mollusc *Ianthina*, and the Tunicate *Salpa fusiformis*.

48. Fassnidge, W. (1932). "Immigrant Lepidoptera: South-East Union of Scientific Societies' immigration records scheme." Entomologist, 65, 164–5.

Numerous additional notes of immigration and variations in abundance, in the same journal, 159, 165–6, 167, 186, 197, 200, 203, 206–11, 282, 284.

49. Chater, E. H. (1932). "Factors determining the distribution of *Apion ulicis*." Nature, 130, 741.

25,500 specimens of this gorse weevil were introduced into an area in Aberdeen where the species does not occur naturally. Some survived for several years, and it is suggested that their absence from certain districts is due either to bad dispersal powers or to periodic cold winters.

50. Parkin, E. A. (1932). "Note on two species of *Lyctus* (Powder-Post Beetles) imported into Great Britain." Ent. Mo. Mag. 68, 277.

An American and a Japanese species which may become established in this country.

Note. Attention is drawn to the *Journal of the Entomological Society of the South of England*, of which Vol. I, No. 1 (24 pp.), was issued in 1932. This contains a large number of valuable short notes on insect ecology which it has not been possible to summarise in these Notices. The *Journal* can be obtained from the Secretary of the Society, 102 High Street, Southampton, and the first number is priced at 2*s*. 6*d*., post free.

REVIEWS

THE FEBRUARY ISSUE OF THE *JOURNAL OF ECOLOGY* (VOL. XXI, NO. 1).

THE current issue of the *Journal of Ecology* contains eleven papers and notes, reviews of Walter's *Hydratur der Pflanzen* and Robinson's *Soils*, as well as reports of meetings of the British Ecological Society, the annual statement of accounts, and the current list of members.

Prof. Thoday deals with the terminology of Xerophytism, suggesting that the word *xerophyte*, with its adjective *xerophytic*, should retain the original use and apply to all plants growing in dry habitats; that *xeromorphic* should be applied to structural characters tending to check transpiration; and that *xeroplastic* should be applied to structures experimentally shown to be produced as a direct result of exposure to dry conditions.

Two papers relate to tropical African regions, Mr J. D. Snowden describing altitudinal zonation on Uganda mountains and Mr P. J. Greenway, the vegetation of Mpwapwa (Tanganyika Territory). To his descriptions of the main plant communities Mr Snowden prefixes a welcome synonymy relating them with previous descriptions. Mr Greenway includes useful climatic data, and follows Phillips in recognising a Deciduous Scrub Formation with *Berlinia-Brachystegia* woodland, and a Sub-tropical Evergreen Forest Formation, which in his area is very poorly developed. Two authors deal with fresh-water aquatic vegetation: Miss Dora Weintroub, who describes the vegetation of the "pans" of the Witwatersrand and accompanying swamps and marshes, and Mr R. W. Butcher, who follows up his earlier account of the vegetation of the River Itchen with a general description of the distribution of macrophytic vegetation in the rivers of Britain. In this he classifies the rivers according to their rates of flow, the nature of their beds, and their lime content, and successfully correlates the vegetation with these conditions. The author has in fact, using a wide range of data, produced an intelligible and natural classification of British rivers as plant habitats, as well as much new information about river vegetation and its communities. Mr G. C. P. Petch contributes an interesting account of the vegetation of St Kilda, a small island in the Atlantic, 50 miles west of the Hebrides, whose population has recently been evacuated. This is intended to supply data with which future developments may be compared. Dr Winifred Brenchley and Miss S. Heintze notice the colonisation by *Epilobium angustifolium* of certain manured grass plots at Rothamsted which have suffered from frost combined with drought, and attribute it to the easing of competition rather than to change of soil reaction. Dr Brenchley and Miss K. Warington publish their second paper on the weed seed population of arable soils and communicate many interesting facts about the relative influence of fallowing and of cultivation under crop on the different weeds. Dr Nellie Carter continues her exhaustive and valuable study of the alga flora of the Canvey and Dovey salt marshes with an enumeration, including detailed accounts of the occurrence and behaviour, of the algal species (about 144 in all, including 80 diatoms). Mr A. C. Joshi suggests a new "explanation" of the prevalence of vivipary in mangroves, and Dr Burtt Davy notes an extension of the range of *Salix* in South America.

A. G. TANSLEY.

A RUSSIAN TEXT-BOOK.

D. N. Kashkarov. *Environment and biocoenosis* (*Foundations of synecology*). Pp. 1–244. Moscow, 1933. (In Russian.)

THIS book represents a course of lectures on the ecology of associations, delivered by the author at the University of Middle Asia in Tashkent, and must be regarded as a very valuable attempt to offer in a condensed form the mass of facts, theories and opinions which constitute this relatively new science. Fundamental theoretical conceptions in ecology

are still very far from being universally recognised, or even understood, and their discussion is greatly desired, particularly when this is done with an open mind and a thoroughly critical attitude to the facts used as arguments. The author of the present book is to be congratulated on producing a lucid summary of the conflicting views of various ecologists, both botanists and zoologists. It is somewhat doubtful, however, whether the book fulfils the requirements of a text-book for students, but this is not the fault of the author, who explains in the preface that the present state of ecology makes it impossible to give definite answers to many problems. This frank recognition of the great inadequacy of our understanding of most ecological problems is very welcome in a book of this kind, since there is already a noticeable tendency amongst ecologists to introduce certain semi-dogmatic ideas and conceptions as the fundamentals of the science. Unfortunately, the author himself did not escape this failing. Thus, his insistence on the rôle of natural selection in the formation of structures and habits of organisms is often very insufficiently supported by facts. For example, when speaking of the pale coloration of desert animals (p. 225) he points out that the protective value of that coloration is not proved, but hastens to suggest that the coloration is a result of some physiological processes which themselves are controlled by natural selection, though this is obviously a theoretical admission not yet tested by study.

Amongst minor faults of the book may be pointed out the very scanty attention paid to modern work on insect epidemiology, in which the all-important problem of fluctuations in numbers has received perhaps the best treatment as compared with similar investigations on other animals. In the discussion of physical factors of environment one misses a heading on the combined effect of the two great factors, temperature and humidity, and the important factor of solar radiation is not even mentioned.

A brief summary of the contents will be sufficient to show the scope of the book. Two introductory chapters include a discussion of ecology and its relation to other sciences, and of the environmental factors. The third chapter is devoted to the environment as it exists in nature, i.e. life zones and habitats; the following four chapters discuss the problem of biocoenoses, their structure, classification, ecology and dynamics. The eighth chapter deals with the quantitative method in the study of biocoenoses; in the ninth, the evolutionary aspect of synecology is discussed. The next chapter is mainly devoted to the economic importance of the biocoenological method. Of particular interest is the eleventh chapter in which various desert biocoenoses are described as an illustration of the main principles exposed in the book; this chapter is largely based on the author's wide experience in Middle Asian deserts. The book concludes with a chapter on methods of synecological work in the field which should be very useful for beginners.

There is no doubt that the book will give a great impetus to the study of ecology in Russia where the extreme diversity of natural conditions make such studies particularly accessible and even necessary, and it is to be regretted that the language in which it is written will make it inaccessible to ecologists of other countries.

B. P. UVAROV.

A CENSUS OF GREBES.

T. H. Harrisson and **P. A. D. Hollom.** *The great crested grebe enquiry*, 1931. British Birds, 26, 62–92, 102–31, 142–55 and 174–95, 1932. (Reprinted: Price 2*s.* 6*d.* H. F. and G. Witherby, 326 High Holborn, London, W.C. 1.)

This conspicuous and elegant fish-eating bird has spread and increased remarkably in Britain during the last fifty years. Given adequate organisation (in which delegation of responsibility to individuals covering smaller districts played an important part), sufficient energy and a modern ecological outlook, this enquiry was assured of the success it has attained. While some of the conclusions drawn from the survey may be questioned in detail, and it does seem likely that in some instances the facts for past years are not sufficiently complete, yet the main results of the census stand out clearly, and may be summarised as follows. In the first place fluctuations in numbers and range have been enormous during the last two hundred years, and were mainly due to natural causes and not to man's

actions. Starting from less than 50 pairs in 1860 the grebe population had increased to over 1150 pairs in 1931. Superimposed on this general trend were smaller fluctuations, of which the decrease of some 55 pairs between 1930 and 1931 is of special interest owing to the fact that spreading continued even while numbers were decreasing (cf. the similar observations by Middleton on the grey squirrel in England, *J.A.E.* 1, 166, 1932). The factors which control choice of habitat are discussed fully, also many other ecological problems. The total fresh-water fish consumption by grebes for England and Wales in one year is reckoned to be nearly a million pounds, and a large amount of this consists of roach and perch. The data on causes of mortality are interesting but quite insufficient to give more than a vague picture of this aspect of grebe ecology. As would be expected, a large mass of information on other matters (courtship, territory, etc.) has been collected during the enquiry (in which over 1300 observers took part), and although the authors may be thought to have under-estimated the difficulty of obtaining conclusive data about the causes of changes in grebe numbers, the facts concerning trends in the population stand out clearly, and form an important basis for future work. As a sheer feat of organisation the enquiry is remarkable. Its success together with that of the previous "British Birds" enquiry into the heron population of Britain (E. M. Nicholson) and of the national grey squirrel enquiry carried out at Oxford (A. D. Middleton) shows what can be done by organising interested observers in a closely populated country like England. In the future it will be very important that such enquiries should be run in such a way that overlapping and competition between different enquiries is avoided, otherwise the amateur naturalist may find himself completely inundated with questionnaires and rise in revolt against them. It is satisfactory to note the full acknowledgments of help recorded in this report, and the completeness with which the results are set forth and analysed.

CHARLES ELTON.

THE FOOD OF BIRDS.

M. L. McAtee. *Effectiveness in nature of the so-called protective adaptations in the animal kingdom, chiefly as illustrated by the food habits of Nearctic birds.* Smithsonian Misc. Coll., 87, No. 7, 1–201, 1932.

SINCE 1885 the U.S. Biological Survey has been engaged in shooting Nearctic birds and analysing and identifying their stomach contents. The collection has now reached the large total of 80,000 stomachs. The present paper is a survey of the results with a view to establishing in what proportions the different divisions of the animal kingdom are eaten. The prey is only analysed to families and the birds are treated as a whole. There is also a large amount of somewhat unbalanced criticism of the theory of protective coloration. Some indication of what this theory really implies may be useful.

The development of protective coloration under the action of Natural Selection postulates that within *one* species there may be several colour-forms, each of which has a certain survival value in relation to the average environment (more particularly predacious enemies) of the species. In the course of time that form which on the whole is best adapted will supplant the other forms. If the environment alters (or the species migrates to a new environment) still another form may become predominant in its turn. The difficulty is that this theory is at present incapable of either proof or disproof and is therefore almost as unsatisfactory as the vitalistic theories of development. Evidently the examination of insect remains in birds' stomachs can scarcely ever throw very much light on the theory, for the material will rarely be sufficiently well preserved. Again, to find that a species *is* eaten is no disproof that its evolution has followed this course; at the most, if we find that a species is *never* eaten, we can only say that selection by predators is not in progress *now*.

McAtee's main argument is that different types of animals are eaten in proportion to their abundance. Unfortunately, the only measure of the abundance of a group is the number of described species it contains. It is a standing reproach to entomologists that no more accurate estimates of numbers are yet possible. With the very rough estimates available it is very difficult to draw any conclusions from the figures. Doubtless they

correct to some extent the exaggerated claims sometimes put forward as to the value of protective colours, stings, odours, etc., in particular groups, but they cannot prove or disprove the essential theory.

On the other hand, there is no doubt that if the Natural Selection theory is to be of any value in biology, its actual working in nature will have to be investigated. Possibly this investigation may be found to lie beyond the reach of human endeavour; if so, so much the worse for the theory. The establishment of the normal food *in nature* of an important predacious group like the Birds is certainly a small step in the right direction. Work such as this, combined with detailed studies of particular species, may in the course of the next few decades show us whether or not it is possible to test the Natural Selection theory. From this standpoint the work of the U.S. Biological Survey is of the greatest value; moreover, the detailed records in their archives are still available for publication. It is the details we want, for McAtee's unparticularised tables are not at present of much use to ecologists.

O. W. RICHARDS.

GAME POPULATIONS.

M. Portal (Chairman of Committee) and **Walter E. Collinge** (Pathologist to the Committee). *Partridge disease and its causes.* Report of the Country Life Committee of Enquiry into the Diseases of Partridges, 1931–2. Pp. 1–96. Price 12*s.* 6*d.* "Country Life," Ltd., London, 1932.

This book summarises the results of an enquiry made by a committee of sportsmen, aided by Dr Collinge, under the auspices of *Country Life*. During 1931 disease was a cause of widespread decrease among partridges in Great Britain, and this enquiry was initiated to find out the nature of the disease and the environmental conditions affecting partridges. Questionnaires were sent to shooting men throughout the country, and dead or diseased birds obtained for laboratory examination. Most of the information collected is summarised in such a form as to indicate the most successful methods of partridge preservation at the present time. There appears to be little doubt that modern agricultural practice, especially the decrease in arable cultivation, is reducing the available life range of partridges and other game; but the influence of particular factors such as poultry-farming, early ploughing of stubbles, tarred roads, carnivorous enemies, artificial manures, winter feeding, etc., can only be debated, as in most cases there is insufficient evidence to reach any clear-cut conclusions. Conclusions based upon opinions and impressions, rather than on facts, must always be open to doubt and argument, until the optimum environmental conditions for partridges and other game are determined by accurate scientific investigation.

The examination of 343 dead or diseased partridges clearly shows that infection with strongyle worms was widespread from 1930 to 1932, and was a cause of great mortality. The worm responsible is *Trichostrongylus tenuis* (Mehlis), closely allied to that (*T. pergracilis*) causing a similar infection in grouse. Dr Collinge succeeded in tracing the life history of this parasite, and found it to be similar to *pergracilis*. The egg stage is passed out with the faeces of the birds and develops on the ground into a free-living larva, which attaches itself in a resting stage to grass, clover, and other ground vegetation; this larval worm, being ingested with the food of the partridge, develops to maturity in the caeca of the birds. These worms do not reproduce within the body of their host, but badly infected birds were found to have 5000–12,000 worms in their caeca. It would appear that the progress of a cumulative parasitic infestation of this nature must be largely dependent upon the density of the partridge population, and to a certain extent upon suitable climatic conditions for the development of the larvae, but little data has yet been obtained on the epidemiological aspect of the problem.

A. D. MIDDLETON.

ANIMAL LIFE ON SAND-DUNES.

Rolf Krogerus. *Ueber die Oekologie und Verbreitung der Arthropoden der Triebsandgebiete an den Küsten Finnlands.* Acta Zoologica Fennica, 12, 1–307, 1932. (English summary.)

This paper is an account of the fauna of the coastal sand-dunes of Finland and is one of the most detailed studies yet made of a habitat of this type. Twenty-six stations with 178 metre quadrats have been examined, covering the stretch of dunes along the Baltic between latitudes 60° and 66° N. The edaphic factors in the habitat are described in great detail and the chief plant communities are indicated. On pp. 140 *et seq.* the author describes experiments on the reactions of the more important members of the fauna to isolated factors. The experiments on temperature reactions are particularly interesting and show that the range in which active life is possible is often rather narrow; in a number of species the lower temperature limit is higher than might be expected.

The Arthropod fauna (insects, spiders, and mites) was examined by means of quadrats or transects at every station. The author's sampling methods are described (pp. 20–4) and are so devised as to give some idea of the relative abundance of species in different habitats, at least when animals of a similar type are compared. Pages 93–133 are occupied by a complete list of the 1443 Arthropods encountered, with an indication as to whether they are xerophilous, littoral or stagnal (marsh-lovers). A number of the species, regarded as xerophilous, are certainly found in woods and damp meadows in England. It is, of course, difficult without a very wide survey to decide which species are confined to a given habitat and which are merely very characteristic of it. The author considers this problem (pp. 194 ff.) in some detail and follows Palmgren in distinguishing between dominance (abundance of an individual species in relation to the total number of individuals) and constancy (the number of samples a species is found in). This use of dominance appears liable to lead to confusion. In plants, dominance usually implies at least some measure of controlling influence in the habitat. It is doubtful or at least not established whether this was ever the case in the so-called dominant animals.

The author has an interesting section (pp. 177–90) dealing with the adaptations of typical sand-dune animals to their environment. There is no doubt that more work of this sort should be done, but great caution is necessary in interpreting the results. For instance, the author shows that a number of typical sand-dune species have a spiny ovipositor for laying the eggs in the sand. But to show that this adaptation is significant, it is necessary to take a wide survey of ovipositor-structure amongst forms living in sand-dunes and amongst those which do *not*. The author certainly shows that some sand-dune forms which probably do not lay in the soil lack the spines, but an examination of forms living in quite different habitats (e.g. *Medetera* spp. laying eggs in rotten wood) would show that they also *have* spines.

It is evident from this brief summary that the paper is a mine of information for those interested in geographical distribution or in the ecology of sand-dunes. But from the standpoint of the general ecologist certain criticisms at once suggest themselves. These arise most naturally in connection with the very beginning of his work (p. 9) where he defines ecology. The following is a free rendering with some omissions: Ecology is the study of the relation between the animal and its environment. The presence or absence of a species from a given habitat depends on the "artverteilenden" (distributional) factors. These can be ranged in two groups: factors which determine whether a species can or cannot live in a habitat (Existenzökologie) and innate factors determining the dispersal of the species (Ausbreitungsökologie). The former is divided further into Autecology and Synecology.

Now there is no reason why with this ground plan the animate part of the environment should be neglected, but it is a fact that it is so to a very large extent. This way of looking at animals has resulted from transferring *en bloc* ideas which are really only applicable to

plants. Amongst the insects (which form the greater part of the fauna described) the relations of one species to another are probably often more important than the relations to the physical environment. At least it appears grotesque to list large numbers of Diptera and Hymenoptera, xerophiles constant to the habitat, without even mentioning that many of the species are only present because they are restricted parasites of other members of the fauna. Doubtless the parasites would not be there if they could not withstand the edaphic conditions, but they would be there even less if the hosts were absent.

The same essentially botanical view-point leads to some neglect of the problem of animal numbers. The data are only treated quantitatively as far as is necessary to prove the habitat constancy of each species. But if the relations of the species to one another were more considered, if the species were more thought of as food for or enemies of their associates, the actual numbers in which each occurred would have a new significance. Admittedly, no technique has as yet been worked out to enable ecologists to discover, much less to exhibit, the interrelations of all the animals living in any but the simplest habitats, but it is doubtful whether the listing of species without considering their effects on one another can take us very far.

O. W. RICHARDS.

A CORAL REEF.

T. A. Stephenson, Anne Stephenson, Geoffrey Tandy and **Michael Spender.** *The structure and ecology of Low Isles and other reefs.* Scientific Reports of the Great Barrier Reef Expedition, 1928–9, 3, No. 2, 1–112. Price £1. British Museum (Natural History), Cromwell Road, London, S.W. 7, 1931.

THERE is no doubt that the reader of this important report will turn first to the maps and photographs, which form a magnificent set illustrating both the general ecological divisions of plant and animal life on this reef, and also some of the characteristic species. These illustrations, together with the clearly written account that precedes them, give a vivid impression of a small reef, less than a mile in length, that has been surveyed by modern ecological methods. The variety of habitats is interesting, including mangrove swamp, rocky shore, a sandy cay where the lighthouse stands, and the diverse regions of the reef-flat and rampart, each with a characteristic set of animals and plants. The collections have been deposited with detailed ecological labels at the British Museum, where they are intended to act as the "vouchers" for future expeditions which may wish to "audit accounts." This procedure might be adopted more extensively by other expeditions, and by people doing ecological surveys in this country. The lists of animals and plants cover those that are characteristic of each habitat. The exact meaning of this term is not made clear, and it would be desirable, when studying associations which cannot through difficulties of time and labour be completely collected, to define more exactly whether "characteristic" means common, exclusive, or conspicuous. Without some such definition close comparison with, e.g., terrestrial associations, is impossible. About 40 species of animals are listed from the mangrove swamps, and about 80 from the reef flats. The algae of this reef are contrasted with those of temperate shores. The reef has few of the abundant higher algae (e.g. fucoids and laminarians) so common in our climate and in the southern temperate region. Corals and alcyonarians practically replace laminarians. But both encrusting nullipores and blue-green algae are very abundant, as are also unicellular species which live in the tissues of corals, molluscs, hydroids, and other animals, and raise the oxygen content of the water to a high level at certain times. Acorn barnacles are largely replaced by the rock-oyster, *Ostrea mordax*. The report also contains discussions of the method of formation of such reefs, the geographical relations of the animals with special reference to echinoderms, and comparisons with other reefs already known or surveyed during the expedition. Other reports already published or in preparation cover the special studies made on these reefs.

CHARLES ELTON.

SUPPLEMENT:
THE BALANCE OF ANIMAL POPULATIONS

By A. J. NICHOLSON, D.Sc.

THE BALANCE OF ANIMAL POPULATIONS

By A. J. NICHOLSON, D.Sc.

(Division of Economic Entomology, Commonwealth Council for Scientific and Industrial Research, Canberra, Australia.)

(With eleven Figures in the Text.)

FOREWORD.

For some years the writer, with the generous collaboration of Prof. V. A. Bailey[1], has been investigating the problem of competition in animal populations. An endeavour has been made to investigate the influence of competition on animal populations in all the principal kinds of situations known to exist between animals, and between animals and their environments, and to examine the major types of other factors known to influence populations, in order to see whether these are capable of nullifying, or otherwise influencing, the effects of competition. The scope of the work is thus very wide, and a full presentation of the conclusions, and of the arguments upon which they are based, cannot be given here.

The present paper forms an introduction to later and more detailed publications. Its object is first, to show why it is believed that the competition existing between animals when searching is of fundamental importance in the limitation of animal populations, and secondly, to give an outline of the major conclusions of biological interest that have been reached. Nothing more is attempted at present than to show the reasonableness of these conclusions, rigorous proof being postponed to future publications. It is thought that the "bird's-eye view" of the subject thus given will not only prepare the way for the more detailed work to be presented later, but will also provide biologists with useful hypotheses, the proof or disproof of which by experiment and observation should materially advance our knowledge of animal populations and their natural control.

PART I. THE NATURAL LIMITATION OF POPULATIONS.

The existence of balance.

It appears to be usual at present to deny the existence of the "balance of nature," about which there has been so much vague talk. Therefore, before considering the question of the balance of animal populations, we must examine the arguments for and against the existence of such balance.

There is an outstanding feature of animal populations with which all must be familiar. In any given place the population densities of animals are ob-

[1] Associate Professor of Physics, University of Sydney.

served to change in close association with the changing seasons. Similarly, for any given species of animal, the population density differs in different places, and usually there is a fairly evident relation between the differences in the population densities and the differences in climate, or other environmental conditions. These observations clearly indicate that animal populations must exist in a state of balance, for they are otherwise inexplicable.

Let us take a simple analogy. A balloon rises until the weight of air displaced exactly balances the weight of the balloon, but if ballast be then discarded the balloon again rises until it reaches a new position of balance. Because a balloon in the air is a balanced system, there is a relation between the weight it carries and the height it reaches; without balance, the height reached would be indeterminate.

The balance of animal populations is similar to that of a balloon acted upon by the changing temperatures of night and day. Such a balloon rises and falls in relation to the change in temperature, for this varies the volume of the balloon and the density of the surrounding air. The balloon is continually in a state of tending towards a position of stationary balance, but continues to rise and fall because the position of stationary balance is changing all the time. It may be remarked that even when moving uniformly the balloon is in a state of balance, friction with the air making up the deficiency either in the weight of the balloon or in the weight of air displaced, so governing the speed with which the balloon rises or falls.

The observed fact that there is a relation between the population densities of animals and environmental conditions can be explained only in terms of balance, just as the relation between the weight carried and the height reached by a balloon can be explained only in this way. Without balance the population densities of animals would be indeterminate, and so could not bear a relation to anything.

The evidence for the existence of balance is not confined to logical deduction from the known facts about animal populations existing in a state of nature. Experiments dealing specifically with populations prove that the latter do reach a state of stationary balance under constant environmental conditions. Thus Pearl (**18**, ch. 2), working with *Drosophila melanogaster* bred on banana-agar in milk bottles, showed that the density progressively approaches an asymptotic population, which is clearly a population in a state of balance. However, owing to difficulties of manipulation, his experiments mostly ended when the asymptotic population was closely approached. It is of particular interest that different races of *Drosophila*, bred under identical conditions, have different asymptotic populations.

Chapman (**3**), working with the flour-beetle, *Tribolium confusum*, showed that populations of this beetle grow until a particular density is reached, beyond which there is no further growth. This density is independent of the absolute quantity of flour available. In other words, the number of beetles is

directly proportional to the quantity of flour available, when a state of balance is reached.

MacLagan (**15**, p. 126), working with *Smynthurus viridis*, has shown that increasing density progressively decreases the rate of population growth, and this is the essential mechanism for the production of balance in populations.

The most satisfactory experimental demonstration of the production of balance in animal populations is given by Holdaway (**9**). He shows that under given conditions populations of *Tribolium confusum* reach and maintain a particular density; and also that when the conditions are varied (he varied humidity) the density reached is also varied. He brings out clearly the important point that it is the interaction of the insects themselves that produces balance and so limits density, while physical factors, by modifying this interaction, influence the position at which the insects themselves limit their population.

Arguments used to disprove the existence of balance in nature.

Having very briefly considered the evidence provided by observation and experiment for the existence of balance in animal populations, let us now examine the arguments that have been used to support the contention that there is no such balance.

The claim that animal populations are not in a state of balance is usually based upon the observation that animals do not maintain constant population densities. Clearly this argument is illogical, for, if a population is in a state of balance with the environment, its density must necessarily change in relation to any changes of the environment. A population density that does not change with the environment is evidently not in a state of balance, but is fixed independently of the environment.

Another argument, which has received much prominence in recent years, is that, because a close association between variations in the population densities of animals and changes in climate has been demonstrated, therefore climate is almost wholly responsible for the determination of the densities of animals—while other factors, such as the availability of food and space, and the presence of natural enemies, are of negligible importance (cf. Bodenheimer (**2**) and Uvarov (**23**)). The fallacy of this argument is made evident by the following analogy: If we examine the surface of the ocean, we observe that it rises and falls in relation to the position of the moon. From this we do not conclude that the depth of the ocean is determined by the position of the moon, but merely that change in depth is associated with the position of the moon. The depth of the ocean is determined by the shape of the ocean bottom, by the quantity of water present, and by the balance of the surface, governed by gravity. Similarly, the observed association between changes in the population densities of animals and changes in climate does not show that the densities are determined by climate, but merely that climate may vary the densities. These, it will be

shown, are determined by other factors besides climate, and are limited and held in a state of balance by competition.

Climate, by itself, cannot determine the population densities of animals, for it does not possess the property necessary for the production of balance; and it has already been shown that, unless there is balance, densities are indeterminate and cannot be related to anything. For the production of balance, it is essential that a controlling factor should act more severely against an average individual when the density of animals is high, and less severely when the density is low. In other words, *the action of the controlling factor must be governed by the density of the population controlled.* Clearly no variation in the density of a population of animals can modify the intensity of the sun, or the severity of frost, or of any other climatic factor. The necessity for this interdependence of population densities and the action of the controlling factors has been pointed out by several writers (cf. Howard and Fiske (**11**, p. 107), Nicholson (**17**, p. 83), Fisher (**7**, p. 42), Martini (**16**)), but its paramount importance in the study of the population problem has generally been lost to sight by biologists.

A moment's reflection will show that any factor having the necessary property for the control of populations must be some form of competition. If the severity of its action against an average individual increases as the density of animals increases, the decreased chance of survival, or of producing offspring, is clearly brought about by the presence of more individuals of the same species in the vicinity. This can only mean that the decreased chance of survival is due to increased competition of some kind.

In recent years the importance of the influence of climate on the activities of animals has been demonstrated by many workers. They have shown that changes in population densities are associated with changes in climate; but, for the reasons just given, this does not support the hypothesis many of them stress so strongly, namely, that the climate is mainly, if not wholly, responsible for the determination of the population densities of animals. The point of view of these workers is well expressed by Uvarov in the following passages: "...the evidence collected in this section, as well as in the whole of this paper, should go far towards proving that the key to the problem of balance in nature is to be looked for in the influence of climatic factors on living organisms" (**23**, p. 161). "It is a balance resembling that of a cork floating on the surface of a running stream, with its whirlpools, eddies and back currents, while the wind blowing with varying force now ripples the surface gently, now causes it to rise and fall in great waves. The cork rises and falls with them, comes into collision with other floating objects, now rides on a calm surface and is dried by the sun, now is again rolled over and over by a storm and is beaten by rain, but always continues its journey with ever-changing velocity and along a fantastically tortuous course" (**23**, p. 162).

This simile is apt, and forcibly illustrates the vicissitudes of an animal

population. But stress is placed on the agitation of the cork, whereas its balance on the surface of the water is fundamentally important. Were it not for this balance, the cork would simply fall out of the system, and its interesting career would be brought to an untimely end. So it is with animal populations. Were it not for the fact that competition holds populations in a state of balance with their environments, there would be no limited populations for physical factors to vary. The populations would either disappear altogether or increase without limit.

In support of the contention that climate is mainly, if not wholly, responsible for the limitation of animal populations, much stress is commonly placed upon the fact that climate is known to destroy large numbers of animals. Quantitative observations in the field have proved that climate sometimes destroys far more individuals of a species than all other factors put together (cf. Bodenheimer (**2**)). However, the belief that this proves the important part played by climate in determining the densities of animals is based upon the confusion of two distinct processes, namely, destruction and control.

Let us take an example to illustrate the distinction between these processes. We will suppose that the animals in a certain population would increase one hundredfold in each generation if unchecked, and also that, on the average, climate destroys 98 per cent. of the animals. It is clear that the number of animals would be doubled in each successive generation if no other factors operated. Climate could never check this progressive increase, for it would continue to destroy only 98 per cent., its action being uninfluenced by the density of the animals. If, however, there is some other factor, such as a natural enemy, the action of which is governed by the density of animals, the destruction of the remaining 1 per cent. necessary to check increase would soon be accomplished. If this example were observed in nature, one would be tempted to conclude that, because climate destroys 98 per cent. of the animals while the natural enemy destroys only 1 per cent., the limitation of the population is mainly due to the influence of climate. However, it is clear that the natural enemy is wholly responsible for control, because climate, by itself, would permit the density of the population to become indefinitely great. It is not even necessarily true that the destruction caused by climate reduces the density of animals. Considerations will be given later which show that in such a situation the effect of climate is almost as likely to increase the number of survivors in an average generation as to decrease this number!

If an attempt be made to assess the relative importance of the various factors known to influence a population, no reliance whatever must be placed upon the proportion of animals destroyed by each. Instead, we must find which of the factors are influenced, and how readily they are influenced, by changes in the density of animals.

Investigations on the influence of climate on the life and activity of animals are in themselves of great interest. Also, they are of great economic import-

ance, for they enable us to predict the possible limits of distribution of pests, and under what conditions increases or decreases in abundance may be expected. But, until such time as they take balance into account, they cannot give us any information about the values at which the densities of animals will be limited under given conditions, and this is the most important problem of all in economic biology.

VIEWS ON THE MECHANISM OF BALANCE.

Having shown that the evidence for the existence of balance in animal populations is overwhelmingly great, and that the arguments commonly used when denying balance are unsatisfactory, we will now examine the views generally held about the mechanism of balance.

In almost all discussions of the "balance of nature" there is a strong implication that evolution is responsible for this. It seems generally to be considered that natural selection is the mechanism of evolution that produces and maintains balance, though how it can do so is never clearly stated. This common belief that natural selection has two distinct functions, namely, selection and the production of balance, appears to be responsible for most of the criticism to which the theory of natural selection has been subjected. Elton clearly recognises the difficulty, and remarks (5, pp. 24–5): "We have had to abandon the simple idea of the balance of nature, which was supposed to be produced by the natural selection of more or less fixed instincts, physiological reactions and structures....I do not wish to cast doubt here on the general ability of natural selection to produce adaptations. I am merely raising the question whether it is able to account for the regulation of numbers in an animal community."

The function of natural selection is to select—not to produce balance. Its mechanism is very simple. All animals produce a surplus of offspring, which is somehow destroyed. Natural selection merely causes a greater proportion of the more perfectly adapted individuals than of the less perfect ones to be amongst the survivors. This tends progressively to improve adaptation, but it has nothing whatever to do with the production of balance or the limitation of populations.

The idea that natural selection produces balance appears to be due to a misconception about the meaning of "adaptation." It seems generally to be thought that adaptation is the precise adjustment of the properties of species so that they balance the inherent resistance of the environment. This idea is expressed by Fisher (7, p. 38) in the following passage: "An organism is regarded as adapted to a particular situation, or to the totality of situations which constitute its environment, only in so far as we can imagine an assemblage of slightly different situations, or environments, to which the animal would on the whole be less well adapted; and equally only in so far as we can

imagine an assemblage of slightly different organic forms, which would be less well adapted to that environment. This I take to be the meaning which the word is intended to convey, apart altogether from the question whether organisms really are adapted to their environments."

Observation and experiment show that such precise adjustment of the properties of animals to those of their environments does not exist. Thus Uvarov (**23**, p. 152) points out that "The common, though never proved, assumption that every organism is perfectly adjusted to its environment, requires a complete agreement between the environmental relations of the insect and its natural enemies, particularly parasites," and investigation has shown that this complete agreement is often lacking. Similarly, MacLagan (**15**, p. 144) has recently shown that no one set of conditions provides the optima of all the physiological processes of *Smynthurus viridis*, so that clearly this insect can never be precisely adjusted to its environment. Also, we know that species range over environments differing markedly from one another. Therefore, if a species be assumed to be perfectly adjusted to one kind of environment, it clearly cannot be so adjusted to the other kinds of environment in which it also occurs.

Adaptation is not the exact balancing of the properties of the environment by those of a species. It is simply the possession by animals of properties that enable them to exist in a given environment. If individuals with improved properties appear, this type ultimately displaces the original normal type of the species, so improving adaptation; but this adaptation has nothing to do with perfect adjustment or balance.

Even if we assume that adaptation is the qualitative balance of the properties of animals and those of their environments, and that this balance can be produced by natural selection, this does not help to explain the limitation of populations—for qualitative balance would be maintained whatever the density of a species might be. That is to say, there would be a neutral equilibrium, leaving the population densities indeterminate.

However, natural selection cannot produce even this neutral equilibrium. A number of arguments in support of this contention might be given, but it is sufficient at present to mention just one. We will assume that a population is in a state of qualitative balance with its environment, and that within the population there are some individuals having a greater survival value than the average. Clearly natural selection should tend to preserve such individuals at the expense of the others. But, if it does so, the properties of the population are improved, so over balancing those of the environment and permitting a progressive and indefinite increase of the population. If natural selection is to produce and maintain balance, in such a situation it must preserve the normal individuals at the expense of those that have the greatest survival value! It is thus evident that natural selection is not only incapable of producing and preserving qualitative balance, but actually, by altering the properties of

populations must eventually tend to destroy any such balance that may already exist.

Lotka (12 and 13) and later Volterra (24–26 and see Chapman 4, pp. 406–411 and Bailey (1)) give mathematical theories which consider that the interaction of animals may itself lead to a condition of balance, and that the position of stationary balance depends upon the properties of the animals the nature of their interaction and the properties of the environment. They also consider that this interaction causes an oscillation about the steady density. However consideration of the mathematical papers of these and other workers must be postponed to subsequent publications, though it may be mentioned now a brief account of the relation of Volterra's work to the present investigation has already been given (Bailey (1, p. 72)).

Other views on the limitation of populations.

Another mechanism of balance is sometimes described, though it is generally put forward as an alternative to what is considered to be the untenable hypothesis of balance in nature. This mechanism is made clear in the following passages: "The organism considered may increase in numbers for a considerable time but it obviously cannot go on increasing indefinitely. As it increases in numbers it necessarily spreads both in space and time, and hence as it spread it moves to points outside the optimum environment, where its rate of multiplication immediately diminishes" (Thompson (22, p. 57)). "When the population increases seriously far above its optimum, there is a shifting of the animals to other places, so that the abnormal density is relieved. ...If the population is less than it might be, the gaps soon fill in from the outside by a similar process of adjustment. Migration in response to an innate sense of harmony with the habitat makes possible a solution of the animal population problem" (Elton, 5, p. 61).

It will be observed that the migration referred to here is not necessarily a concerted movement of a large number of a population to a distant place, but is more likely to be a diffusion of individuals within, or beyond, the normal area of distribution of the species. The migrating animals may reach new and unoccupied suitable places outside the boundaries of their normal area, but in general they are likely to spend their time in unsuitable places, so that their chance of survival is reduced. In short, pressure of population induces migration, and this in turn decreases the chance of survival of an average individual. Thus the mechanism possesses the property essential for the limitation of populations, and automatically causes a population always to tend towards a position of balance.

It is of interest to note that with this mechanism it is possible that the whole of the surplus animals may be destroyed by climatic factors, and yet climate is not responsible for control. If increasing pressure of population in favourable areas leads to migration, the degree of migration is governed by the

severity of competition. The proportion of individuals destroyed by climate is dependent on the proportion competition forces out of the favourable parts of the environment. Therefore it is competition, not climate, that regulates the fraction of animals destroyed, and so limits the density and holds the population in a state of balance with the environment.

Mention needs to be made of Chapman's concept of "biotic potential," which he defines as "the inherent property of an organism to reproduce and to survive" (**4**, p. 182). His idea appears to be that biotic potential, when pitted against environmental resistance, determines the density of a species; and that, as biotic potential and density can be measured, environmental resistance can be expressed quantitatively in terms of these factors. Space does not permit of detailed discussion of his arguments, so attention will be confined to his main thesis, namely, that the resistance of the environment to organisms is similar to the resistance of a conductor to an electric current. The reader is expected to see a striking resemblance between electrical potential (i.e. work done on a unit electric charge) and biotic potential (i.e. *possible* rate of increase). The whole argument seems to depend upon this double use of the word "potential."

Chapman continually reiterates the importance of his hypothesis in enabling us to express biotic factors in a quantitative way. However, he makes only one attempt to give an example of such quantitative expression. Having experimentally determined the density of *Tribolium confusum* under certain conditions, he proceeds to calculate environmental resistance by means of his formula. A glance at this example (**3**, p. 120) shows that the only use made of the experimentally determined density is to multiply *both* sides of the equation by it. Clearly the result is independent of density, and Chapman's hypothesis completely fails to help us to deal quantitatively with animal populations.

Competition.

It has already been shown that competition is capable of producing balance, and so of limiting animal populations. Indeed, any factor that produces balance is almost necessarily some form of competition, for balance can be produced only if increasing density decreases the chance of survival of an average individual. There is, of course, nothing new in the idea that competition is the major factor limiting populations, for this idea is fundamental to the epoch-making work of Malthus (**14**) on the population problem.

Many organisms alter the chemical and physical nature of their environment, and, generally, the increase in density of such organisms causes the character of the environment to become progressively less suitable for themselves. This clearly is a form of competition and provides the mechanism necessary for balance. It appears to be of major importance in the control of plants and micro-organisms, and not only limits the densities of species but also plays an important part in determining what other species may exist in the

same environment. Competition of this type is sometimes also of importance to animals. For example, by destroying vegetation grazing animals alter the light, humidity and other physical factors near the ground, so making the environment unsuitable for many animals and plants that live on or close to the ground, while making it suitable for other animals and plants that would have been unable to live in the shade of the vegetation. Thus the alteration of the physical qualities of the environment by the activities of animals may be of the utmost importance in determining what kinds of animals can live together in any given environment.

Though a species may sometimes limit its own density by altering the chemical and physical qualities of its environment, such limitation seems to be unusual amongst animals. Generally speaking, animals appear to be limited in density, either directly or indirectly, by the difficulty they experience in finding the things they require for existence, or by the ease with which they are found by natural enemies. We are thus faced with the problem of the competition that exists amongst animals when searching, and the whole of the investigation that follows is concerned with this important problem.

Examination of the problem of searching shows that it is fundamentally very simple, provided the searching within a population is random. Before further investigation, therefore, we must find if it may safely be claimed that the searching within animal populations is actually random.

It is important to realise that we are not concerned with the searching of individuals, but with that of whole populations. Many individual animals follow a definite plan when searching. For example, a fox follows the scent of a rabbit, and a bee systematically moves from flower to flower without returning on its course. However, there is nothing to prevent an area that has been searched by an individual from again being searched systematically by another, or even the same, individual. If individuals, or groups of individuals, search independently of one another, the searching within the *population* is unorganised, and therefore random. Systematic searching by individuals improves the efficiency of the individuals, but otherwise the character of the searching within a population remains unaltered. Therefore, when investigating the problem of competition, we may safely assume that the searching is random.

We will now examine this question of random searching. The area searched by animals may be measured in two distinct ways. We may, as it were, follow the animals throughout the whole of their wanderings and measure the area they search, without reference to whether any portions have already been searched, and so measured, or not. This we will call the area *traversed* by the animals. On the other hand, we may measure only the previously unsearched area the animals search. This we will call the area *covered* by the animals. Thus the area *traversed* represents the total amount of searching carried out by the animals, while the area *covered* represents their successful searching, i.e. it is the area within which the objects sought have been found.

Suppose we now take a unit of area, say a square mile, and consider what happens at each step when animals traverse a further tenth of that area. When the animals begin to traverse the first tenth of the area, no part of the area has already been searched, so in traversing one-tenth the animals also cover one-tenth of the area. At the beginning of the next step only nine-tenths of the area remains unsearched, so, as the animals search at random, only nine-tenths of the second tenth of the area they search is previously unsearched area. Consequently after traversing two-tenths of the area the animals have covered only 1·9-tenths. Similarly, after traversing three-tenths of the area the animals have covered only 2·71-tenths. The calculation may be continued in this way indefinitely, and it is clear from the character of the problem that, at each step of one-tenth of area traversed, the animals cover a smaller fraction of area than in the preceding step. Also, because at each step the animals cover only one-tenth of the previously unsearched area, the whole area can never be completely searched. This, however, is true only if the total area occupied by the animals (not the unit of area considered) is very large. When the results of such a pro-

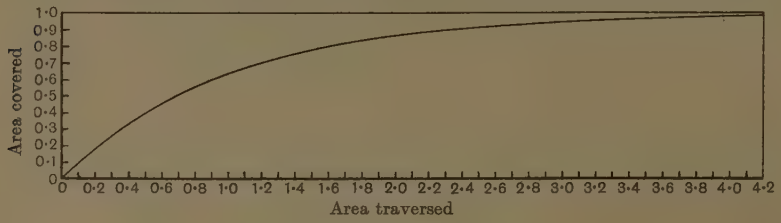


Fig. 1. The "competition curve."

gressive calculation are plotted, they are found to approximate to the curve shown in Fig. 1.

Such a calculation gives the general character of the effects produced by progressively increasing competition, and the original work on the present investigation was based on a curve calculated in this way. However, such a curve only approximates to the true form. Thus, when the animals have nearly completed their search of the first tenth of the area, only slightly more than nine-tenths of the area remains unsearched. Consequently even while traversing the first tenth of the area the animals spend some small part of the time searching over areas that have already been searched, and the same type of error runs through the remainder of the calculation. The calculation could give the correct result only if it were based upon indefinitely small steps. For this reason I approached Prof. V. A. Bailey, who gave me the formula (see Bailey (**1**, p. 69)) upon which the "competition curve" shown in Fig. 1 is based. This curve was then used throughout the investigation.

It may be mentioned that Fiske (**8**) used a curve, based on arithmetical calculations, which was essentially similar to the "competition curve," and that

Thompson (**21**) made use of a formula (given him by Prof. Deltheil of Toulouse) virtually the same as that on which the "competition curve" is based. However, both these authors were concerned only with the problem of superparasitism, a very specialised form of competition, and neither attempted to use the curve or formula for the investigation of the general problem of competition.

Examination of Fig. 1 shows that as the area traversed increases there is a progressive diminution in the rate of increase of the area covered. That is to say, the searching animals have progressively increasing difficulty in finding the things they seek. This is shown more directly in Fig. 2, which is easily derived from Fig. 1. Thus there is a definite relation (expressed in Fig. 2) between

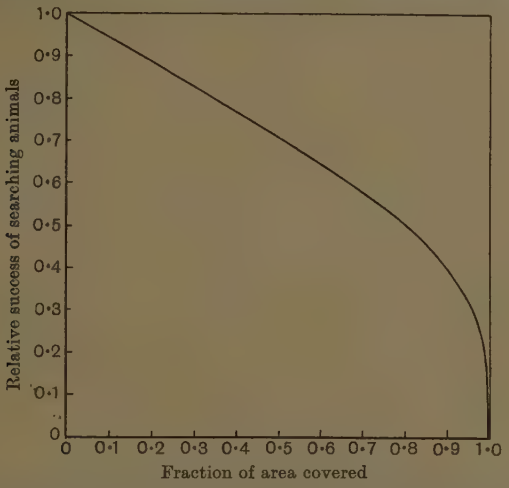


Fig. 2. Curve showing how increasing intensity of competition decreases the success of an average individual in finding the things it seeks. The success of an individual when free from competition is represented by unity.

the reduction of the success of the searching animals and the increase of the intensity of competition; and, with random searching, this relation is perfectly general, and so is independent of the properties of animals and those of their environments. Consequently, the "competition curve" has a general application to all problems of random searching.

It should be noticed, however, that the "competition curve" represents a probability. If small numbers of animals and small areas are taken, it is likely that the relation between the area traversed and that covered will not be found to be exactly as shown in Fig. 1. This does not indicate that there is anything wrong with the "competition curve," but merely that small samples of a statistical population are not necessarily completely representative of the large population from which they are taken. As in the present investigation

we are always concerned with large populations, it is safe to conclude that the probability represented by the "competition curve" corresponds closely to what actually takes place in nature.

Before making use of the "competition curve" to investigate the limitation of the densities of animals it is necessary to define certain properties.

The number of times a population of animals would be multiplied in each generation, if unchecked, will be referred to as the *power of increase* of the species under the given conditions. The value of this property determines the fraction of the animals that needs to be destroyed in each generation in order to prevent increase in density.

The area *effectively* traversed by an average individual during its lifetime will be referred to as the *area of discovery* of the species under the given conditions. For example, if an average individual fails to capture, say, half the objects of the required kind that it meets, then the area of discovery is half the area traversed. The value of the area of discovery is determined partly by the properties of the searching animals, and partly by the properties of the objects sought. Thus it is dependent upon the movement, the keenness of the senses, and the efficiency of capture of an average individual when searching, and also upon the movement, size, appearance, smell, etc., and the efficiency in resisting capture of an average object of the kind sought. Consequently, under given conditions, a species has a different area of discovery for each kind of object it seeks. The value of the area of discovery defines the efficiency of a species in discovering and utilising objects of a given kind under given conditions, and determines the density of animals necessary in order to cause any given degree of intraspecific competition.

It is particularly important to recognise that these two properties respectively embrace all those things that influence the possible rate of increase of the animals, and all those that influence the efficiency of the animals in searching. Thus they are not merely properties of species, but properties of species when living under given conditions—the same species may have different properties in different places, or in the same place at different times. Also, it is important to notice that climatic conditions and other environmental factors play their part in determining the values of these properties, for they influence the vitality and activity of animals. Consequently, though such factors may not be specifically mentioned, they appear implicitly in all investigations in which values are given to the powers of increase and areas of discovery of animals.

Further increase of a population is prevented when all the surplus animals are destroyed, or when the animals are prevented from producing any surplus. When this happens the animals are clearly in a state of stationary balance with their environments, and maintain their population densities unchanged from generation to generation under constant conditions. This will be referred to as the *steady state*, and the densities of the animals when at this position of balance as their *steady densities* under the given conditions.

It is a relatively simple matter to determine the steady densities of animals when we know the values of their areas of discovery and powers of increase. Let us take a simple example. We will suppose that an entomophagous parasite attacks a certain species of host, that one host individual provides sufficient food for the full development of one parasite, that the area of discovery of the parasite is 0·01, that the power of increase of the host is 50, and that no factors operate other than those specifically mentioned. Clearly the steady state will be reached when the parasites are sufficiently numerous to destroy 49 out of every 50 hosts, and when there are sufficient hosts to maintain this density of parasites.

The parasites, then, are required to destroy 98 per cent. of the hosts, and so to cover 0·98 of the area occupied by the animals. To do this, it is necessary for the parasites to uncover an area of 3·92, as will be seen from examination of the "competition curve" (Fig. 1).

The required density of parasites, therefore, is $3{\cdot}92/0{\cdot}01$, i.e. 98 approx.[1]

But, in order that the density of the parasites may be maintained exactly, each parasite is required to find on the average one host.

Hence, the parasites are required to find 98 hosts in the area of 0·98 they cover, so that the steady density of hosts is $98/0{\cdot}98$, i.e. 100.

The steady densities calculated, of course, are the number of animals per unit of area. It is always convenient to choose a large unit for the measurement of area, so that the areas of discovery of the animals are represented by fractions, for the densities of animals can then be given in whole numbers. If small units of measurement are used the character of the results obtained is actually unaffected, but the densities calculated have to be expressed as small fractions of an animal per unit of area, which is undesirable.

It should also be noticed that the densities calculated are those within the areas in which the animals increase, and not necessarily within the whole countryside. Thus, if the animals can live only in areas containing a certain kind of vegetation, then the calculated densities are those within such areas, while the intervening areas in which the vegetation is unsuitable for the animals are ignored. Other things being equal, then, the density of a species within the whole countryside varies directly with the fraction of the countryside that provides suitable conditions for the species. It will be shown later that this is only approximately true.

The example just given is an exceptionally simple one, but it illustrates how the problem of the competition of animals may be investigated mathematically. By assuming different properties for the animals, and different kinds of association between animals, or between animals and their environments, it is possible in this way to investigate how competition influences the

[1] Though only the female parasites search for hosts, it is convenient to consider the searching of an average individual with males and females being omitted when making the average, and so estimating the value of the area of discovery.

densities of animals in all the principal types of situation known to exist in nature. Originally this arithmetical method was used for the investigation of almost all the problems that are here presented, but it is cumbersome and makes an adequate presentation of the subject very difficult. I therefore placed the problems before Prof. V. A. Bailey, who undertook the onerous task of investigating them mathematically[1]. The results obtained arithmetically were confirmed by the mathematical investigation, and the work was extended to certain problems that were not amenable to the arithmetical method.

In order to make any progress it was clearly necessary first to investigate ideally simple situations, even though these may have no counterpart in nature. Later, new factors were introduced, one at a time, in order to see how these influence the results already obtained. In this way the major types of factors known to influence animals were investigated. Unless some important factor capable of nullifying the effects of competition has been overlooked, which seems unlikely, the results should correspond to the facts of nature, for we know that animals do search for the things they require, and that competition does exist. It will later be seen that in their general features the results obtained in this investigation correspond to the observed facts, but more detailed observation and experiment is necessary in order to show whether there is a similar correspondence in detail.

The more important conclusions that have been obtained by a study of the problem of the competition that exists between animals when searching are given in Part II of this paper. These conclusions inevitably follow from the formulation of the problem already given, but for their rigorous proof much use needs to be made of mathematics, and it is thought desirable to postpone this to subsequent publications. However, when possible, brief general arguments are given to show that the conclusions are entirely reasonable.

PART II. THE EFFECT OF COMPETITION ON THE DENSITIES OF ANIMAL POPULATIONS.

In this part we shall investigate the way in which competition may determine the densities of animal populations in the types of situation that are believed to be of greatest importance under natural conditions. It must be realised, however, that though natural enemies and the availability of food and of suitable locations are factors that *may* control the densities of populations, they are not *always* control factors. For example, a species that is controlled by the availability of suitable locations is unaffected by the attack of a natural enemy if the latter merely destroys some of the surplus individuals that otherwise would die for lack of suitable places in which to live.

[1] Though arithmetic is a branch of mathematics, it is convenient in this paper to speak of *arithmetical* work when the arguments are conducted on definite numerical examples, and of *mathematical* work when the reasoning is by means of mathematical symbols.

(1) TWO CONCLUSIONS OF FUNDAMENTAL IMPORTANCE.

It has been shown (pp. 135 and 142) that intraspecific competition acts to populations in the way necessary to produce balance, and it is clear that the position of stationary balance is that at which the surplus animals are destroyed, or at which no surplus of animals is produced. This leads inevitably to the following conclusion:

C 1. Intraspecific competition automatically regulates the severity of its action to the requirements of each population, provided the inherent resistance of the environment is sufficiently low to permit the species to exist.

This means that, if animals find an environment suitable for their existence, they will increase in density until such time as the severity of competition, together with the inherent resistance of the environment, just counterbalances the innate tendency of the animals to increase in density. For example, let us suppose that conditions are suitable for the existence of a certain species of natural enemy. In this situation competition influences the density of prey available to the natural enemies. Starting with few natural enemies, their density (and consequently competition) increases until the density of prey is such that the surplus natural enemies fail to find sufficient prey for survival. Clearly, then, if individual natural enemies require large numbers of prey, decrease in the density of prey is arrested when there is a just sufficiently high density of prey for the requirements of the natural enemies. Similarly, when individual natural enemies require very small numbers of prey, balance is reached when the density of prey is very low. This is only one of a number of apparently paradoxical conclusions that follow immediately from *C* 1.

C 2. For the steady state to exist, each species must possess some advantage over all other species with respect to some one, or group, of the control factors to which it is subject.

A *control factor* is one which responds to increase in the density of a given species either (1) by increasing the severity of its action against the species (as do natural enemies), or (2) by causing intraspecific competition to decrease the chance of survival of individuals (as do limited supplies of food or of suitable places in which to live). It should be noticed that (1) is actually a special case of (2).

When the conditions of *C* 2 are not fulfilled, other species maintain the action of all the control factors to which a given species is subject at a greater severity than this species can withstand. Moreover, even when these conditions are fulfilled the given species may not be able to exist in the steady state, for its special advantage with respect to certain of its control factors may be more than counteracted by special disadvantages with respect to other control factors. However, if the species is not so affected by disadvantageous characters, its density tends to reach such a value that intraspecific competition, together with environmental resistance (which includes that due to the

presence of other species), just balances its natural tendency to increase in density.

(2) The interaction of parasites and hosts.

Entomophagous parasites (which are really predators of a special kind) possess certain properties that make the investigation of their competition comparatively simple. They can produce offspring only when they find hosts. Consequently the number of offspring they produce is directly dependent on the number of hosts they find, and the number of hosts they destroy is also directly dependent on the number they find. This is strictly true only on the assumption that parasites possess an unlimited supply of eggs, but investigation has shown that unless the number of eggs produced is very small, the limitation of the egg supply affects the steady densities of the animals so little that it may be neglected. It is of interest to note that one of the fundamental hypotheses of Volterra's work (**24–28**) is that the number of offspring produced by predators is proportional to the number of encounters with prey. Consequently, though he speaks of the "eating species" (*specie mangiante*) and the "eaten species" (*specie mangiata*), he actually deals with parasites possessing an unlimited egg supply. Predators (using the term in its generally accepted sense) do not eat prey in proportion to the number found, for hunger and satiety commonly determine whether the prey met are eaten or not. Similarly, the number of offspring produced, though it may be influenced, is clearly not proportional to the number of prey eaten by a predator.

Because of this direct dependence of the number of hosts destroyed, and of the number of offspring produced by parasites, on the success of the parasites when searching, the arithmetical and mathematical investigations of the interactions of animals have been mainly devoted to the interaction of hosts and parasites. So far it has not been found possible to formulate the problem of the interaction of true predators and their prey in a completely satisfactory way for mathematical treatment. However, the investigation of the special kind of predators we here call parasites (i.e. entomophagous parasites), makes it possible for us to deduce the kind of effects that should be produced under given circumstances when true predators and their prey interact, as will shortly be shown.

For arithmetical convenience it was found necessary to confine attention to what may be referred to as the problem of "discontinuous generation." That is to say, a definite succession of generations was assumed: so, for example, it was considered that all parasite eggs are laid at the same time, and that all the hosts reach the vulnerable stage simultaneously. The mathematical treatment was also mainly devoted to this problem, but later Prof. Bailey extended the investigation to the problem of "continuous generation" (**1**), that is to say, the problem of interacting animals that may reach any stage of their life cycles at any time. Actually the "discontinuous problem" is a special case of the "con-

tinuous problem." However, it should be noticed that "discontinuous generation" approximates closely to what we know to happen commonly amongst animals in nature, and notably amongst insects, to which this portion of the investigation particularly applies. The "continuous problem" will not be presented in this paper, for it can be investigated only by the use of mathematics, but it may be remarked that the conclusions reached are in agreement with those obtained by the investigations of the "discontinuous problem."

Before proceeding to examine the question of the interaction of hosts and parasites, it is necessary to define several convenient terms.

A *specific parasite* is one that attacks only a single species of host; a *general parasite* is one that attacks several species of hosts; and a species of parasite that attacks several given species of hosts is said to be a *common parasite* of the given hosts. Similarly we speak of specific, general and common hosts, according as they are attacked by one species, by several species, or by several given species of parasites. It should be particularly noticed that these relations refer only to the given environment. Thus a parasite known to attack many species of hosts is a specific parasite in a given environment when it attacks only one species of host there.

The steady density of a species at the beginning of a generation is referred to as the *initial steady density*, and that at the end of a generation as the *final steady density* of the species under the given conditions.

We will first confine attention to the steady state, leaving till later the question of whether animals do actually maintain their respective steady densities, and also postponing the investigation of the oscillations in density that occur when hosts and parasites interact.

A. *The steady state.*

(*a*) *The interaction of a specific parasite and a specific host.*

The steady state exists when there is a sufficient density of parasites to destroy exactly the surplus of hosts produced, and when there is a sufficient density of hosts exactly to maintain the density of parasites necessary to destroy this surplus. Thus there is a mutual adjustment of the steady densities of interacting hosts and parasites; the parasites destroy the surplus hosts, and the hosts maintain the parasites while preventing any surplus of parasites from being produced.

The power of increase (see p. 144) of the host species determines what fraction of the hosts the parasites must destroy in the steady state, and so also determines what fraction of the environment the parasites must cover (see p. 142). It is clear that there is only one density at which parasites with a given area of discovery can exactly cover a given fraction of the environment, so it follows at once that:

C 3. The steady density of a parasite species depends alone upon its area of discovery and the fraction of hosts that is required to be destroyed in the steady state.

From this conclusion a number of others may readily be derived.

C 4. The steady density of a host species varies inversely as the number of parasites that develop at the expense of a single host individual.

Thus, if twice as many parasites can develop at the expense of a single host individual, only half as many hosts are necessary to support the steady density of parasites. So, because at this density the parasites destroy the surplus fraction of hosts, it is clear that the steady density of the host species is halved.

C 5. If some parasites are destroyed during development, the steady density of the parasite species is unaltered, but that of the host species is increased, and varies inversely as the fraction of parasites that escape destruction before maturity.

No matter how many parasites are destroyed during development, the same density of mature parasites is required in order to find and destroy the surplus of hosts. Consequently there must be a sufficient density of hosts to support the parasite offspring that are destroyed, in addition to those that ultimately survive.

C 6. The steady density of the host species and that of the parasite species vary inversely as the area of discovery of the parasite species.

If the area of discovery of the parasite species is doubled, then only half the density of parasites is necessary in order to find the surplus hosts, and so half the density of hosts supports the required density of parasites.

C 7. Reducing the power of increase of a host species decreases the initial steady density and increases the final steady density of the host; it also decreases the steady density of the parasite species.

It is easy to see that the steady density of parasites should be reduced, because, for balance, they are required to destroy a smaller fraction of hosts, and they can do this only if their density is reduced. Also, it is clear that the initial steady density of hosts should be reduced, for a lower density of hosts supports the required density of parasites. However, the parasites leave a larger fraction of a reduced density of hosts, and it is impossible to show by means of simple argument whether this means that the final steady density of hosts is increased or decreased. A special numerical example, illustrated in Fig. 3, is therefore used in order to show that the final steady density of hosts is increased. The curves in this figure may be derived easily from the "competition curve" (Fig. 1) by means of simple arithmetical calculations. Thus great fecundity itself *tends* to decrease the density of survivors.

C 8. The steady density of a parasite species is lowered when some of the hosts are destroyed by factors other than the parasite.

Clearly the destruction of some of the hosts by some other factor reduces the fraction of hosts to be destroyed by the given parasite. In other words, the *effective power of increase* of the host, with reference to the given parasite species, is reduced. The arguments supporting *C* 7 therefore also apply here.

C 9. According to whether a destructive environmental factor operates before, after, or at the same time as a given parasite species, both the initial and final steady densities of the host species are respectively lower than, higher than, or the same as they would be if the parasite were alone responsible for destroying the surplus hosts.

The destruction of some of the hosts by another factor clearly reduces the effective power of increase of the host with reference to the given parasite. Consequently the parasites are required to commence to operate in a lower density and to leave a higher density of hosts than they otherwise would (*C* 7). If, then, the parasite operates after the other destructive factor, the density of hosts reaching the stage attacked by the parasite is decreased, the final steady density of hosts is increased and the initial steady density of hosts is also

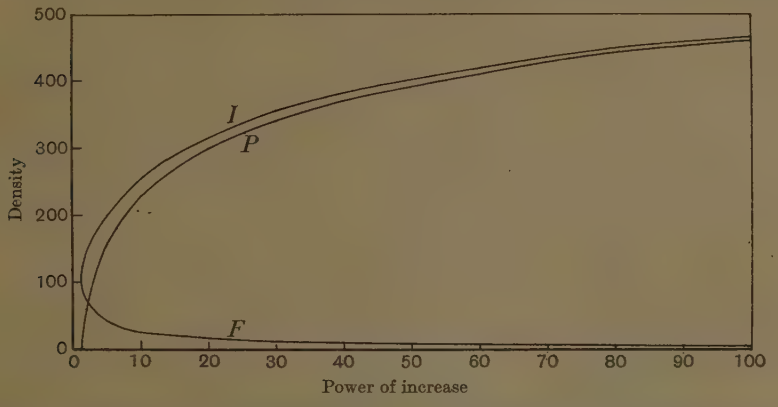


Fig. 3. Area of discovery of parasite species 0·01. *I*, the initial, and *F*, the final steady density curve of the host-species. *P*, the steady density curve of the parasite species.

increased, for the true power of increase of the host is unaltered and the initial steady density is equal to the final steady density multiplied by the power of increase. Similarly, if the parasite operates before the other destructive factor, the initial steady density of hosts is clearly decreased, and the final steady density of hosts, left after the operation of the other destructive factor, is also decreased. When the other destructive factor operates at the same time as the given parasite, the situation is evidently intermediate between the two just examined, so one might expect that there would be little, if any, change in the density of the host. However, to prove that the density of the host is actually unaltered does not appear to be possible without the use of mathematics, or of numerical examples.

C 10. The steady density of a host species is but little increased owing to the limitation of the egg supply of its parasites, unless the maximum number of eggs a parasite may lay is very small.

In the steady state on the average (including males and females) a parasite is required to lay only one egg. It is easy to show that, with random distribution, the number of parasites required to lay more than five eggs (say, 10 eggs per female) is extremely small. The egg supplies of parasites are much greater than this, so unless there is an extremely high mortality before the parasites reach maturity, it is unlikely that the limitation of the egg supply will make any appreciable difference in the number of hosts destroyed. However, it should be noticed that during violent fluctuations the abundance of hosts may so greatly exceed that of their parasites that the parasites are unable to attack all the hosts they find. If so, the rate at which the parasite population catches up to that of the hosts may be somewhat retarded, but even so the steady densities of the animals are unaltered.

(*b*) *Several specific parasites attack a common host.*

C 11. When several species of specific parasites simultaneously attack a common host species, the steady state is practically impossible.

It is inconceivable that the properties of two or more species should be identical. Consequently, when several species of specific parasites simultaneously attack a common host species, that parasite which is capable of maintaining the steady density of the host at the lowest value must inevitably and completely displace the other species of parasites, however slight its advantage may be. This is because individuals of the most potent species compete for the same hosts as do individuals of the other parasite species, and so at all times have a greater chance of producing offspring. The consequent reduction in the densities of the less potent species does not reduce the severity of the competition to which they are exposed, for this is maintained by the most potent species.

C 12. If several species of specific parasites attack a common host species in succession, the steady state may exist, provided each species of parasite has a greater area of discovery than that of the parasite preceding it in the series.

A parasite species that attacks a common host species at a later stage in its life cycle than do other parasites has the special disadvantage of being able to attack only such hosts as are left by the preceding parasites. Each species of parasite operates in a lower density of hosts than does the preceding parasite, so it is conceivable that the special disadvantage of operating in a lower density of hosts might be counterbalanced by the possession of a greater area of discovery than that of the preceding parasite. Actually a precise counterbalancing of the special disadvantage by the value of the area of discovery is not essential, for competition provides a mechanism of adjustment. Each species of parasite operates at a time when there are no other parasites, so an increase or decrease in its density varies the success of an average individual in finding hosts. Consequently an adjustment of the density of each of the species of parasites may permit a state of balance to exist. Clearly, however, there must be a limit to the possibility of such adjustment, for any one of the parasite species may have

such an area of discovery that even in the absence of intraspecific competition its efficiency is less than sufficient to counterbalance that of the other parasite species.

Consequently:

C 13. For the steady state to exist, the relative values of the areas of discovery of successive parasite species must lie between certain limits.

The limits of the permissible areas of discovery of parasites in a special numerical example involving two parasite species are shown in Fig. 4. The curves in this figure may be derived fairly easily from the "competition curve"

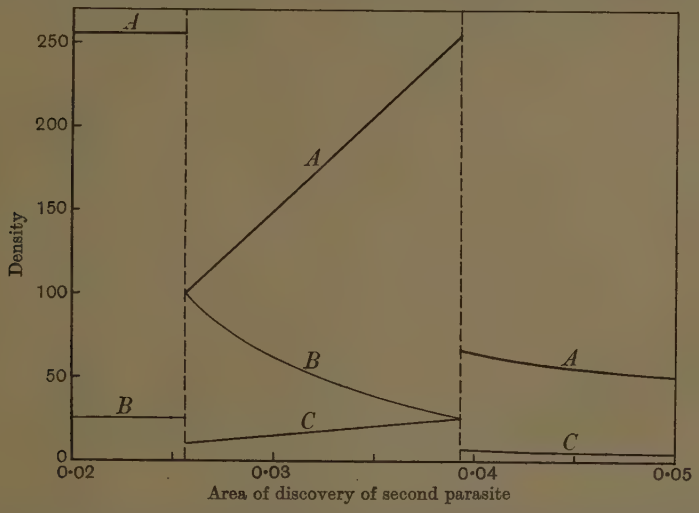


Fig. 4. Power of increase of host species 10. *A*, initial steady density curves of host species. *B* and *C*, steady density curves of hosts left respectively by the first and second parasite species. The region in which balance is possible between the two parasite species is delimited by dotted lines.

(Fig. 1) by means of arithmetical calculation. It will be observed that the second parasite can operate in association with the given first parasite only when its area of discovery lies between 0·0256 and 0·0392. When the area of discovery of the second parasite is less than 0·0256 the first parasite is relatively too powerful, and so operates alone, while when its area of discovery is more than 0·0392 the second parasite is so powerful that it displaces the first parasite.

C 14. As the area of discovery of any one of several successive species of specific parasites is increased, the density, and the fraction, of hosts attacked by this parasite is decreased.

This is clearly illustrated by Fig. 4 and by other numerical examples that have been examined, but its general truth can be proved only by the use of

mathematics. Though this conclusion at first seems paradoxical, it is actually only an extension of *C* 6.

C 15. As the area of discovery of any one of several successive species of specific parasites is increased, the steady density of this parasite decreases.

This follows at once from *C* 14, and is an extension of *C* 6.

C 16. As the area of discovery of any one of several successive species of specific parasites is increased, the initial and final steady densities of the host are equally as likely to be increased as decreased.

For the rigorous proof of this conclusion it is necessary to use mathematics. However, the middle part of Fig. 4 illustrates the more paradoxical part of the conclusion, namely, that the initial and final steady densities of a host may be increased as a result of an increase in the area of discovery of one of its parasites. Whether an increase or a decrease in the initial and final steady densities of a host is produced is dependent on whether the given parasite occupies an even or an odd position in the series of successive parasites. More detailed investigation shows that the steady density of the host at any other stage of its life cycle may be either increased or decreased, according to the circumstances, by the increase in the area of discovery of one of the parasite species.

C 17. When a new specific parasite species is introduced to attack a host species, that is already attacked by specific parasites, the density of the host at the stage attacked by the introduced parasite is increased.

Fig. 4 shows that when the area of discovery of a parasite has the highest permissible value, the parasite destroys no hosts and so is present in indefinitely small numbers. The general truth of this has been proved mathematically, and it may be inferred from *C* 15. We may reasonably assume that the situation before the introduction of a new parasite is essentially the same as if the new parasite were present in indefinitely small numbers, its area of discovery having the highest permissible value. The reduction of the area of discovery of this parasite to such a value that the parasite can destroy some of the hosts (see *C* 14) is equivalent to the introduction of the new parasite. As the parasite originally found no hosts, when its area of discovery had the highest permissible value, but is caused to find an appreciable number when its area of discovery is reduced (i.e. when the new parasite is introduced), it is clear that a higher density of hosts must reach the stage it attacks. This is illustrated by Fig. 4, for it shows that, in the presence of the second parasite, the first parasite always leaves a higher density of hosts than it does when it operates alone.

C 18. When a new specific parasite species is introduced to attack a host species already attacked by specific parasites, the initial and final steady densities of the host may be either increased or decreased.

This follows from *C* 16, for it has been shown (*C* 17) that the introduction of a parasite is equivalent to lowering the area of discovery of a parasite from

its highest permissible value. More detailed investigation shows that the introduction of a new parasite may either increase or decrease the density of the host species at any stage of its life cycle, other than that attacked by the introduced parasite.

C 19. As the power of increase of a host species is raised, the densities of hosts left by alternate species of specific parasites, including the last in the series, are decreased, while the densities of hosts left by the remaining parasites are increased.

Mathematical or arithmetical investigation is necessary for the proof of this conclusion. For a particular numerical example, it is illustrated by Fig. 5, which has been derived arithmetically from the "competition curve" (Fig. 1). It

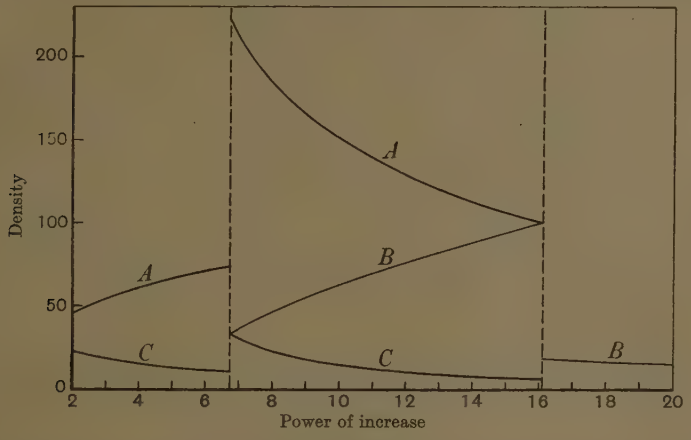


Fig. 5. Area of discovery of first parasite species 0·01, and of second parasite species 0·03. *A*, initial steady density curves of host species. *B* and *C*, steady density curves of hosts left respectively by the first and second parasites. The region in which balance is possible between the two parasite species is delimited by dotted lines.

will be observed that the steady state for the two given parasites and the given host is possible only between certain limits, that is, when the power of increase of the host lies between 6·7 and 16·1. It follows that:

C 20. When the power of increase of a host species is modified, the steady state between species of specific parasites that attack it may be rendered impossible, though this was previously possible.

A general conclusion of importance to subsequent investigations is that:

C 21. As the area of discovery of any one of several species of specific parasites that attack a common host species is increased, the number of hosts attacked by the given parasite in the steady state is decreased, whatever may be the relation in time between the given parasite and the other parasites, provided that the steady state is maintained by all the interacting animals.

This has already been shown to be true when several species of specific parasites attack a common host species in succession (C 14). More detailed investigation shows that this is also true when the various species of parasites attacking a common host species have overlapping periods of attack, and when the parasites attack the common host simultaneously. In spite of C 11, the latter situation is of some importance to subsequent investigations.

(a) Several specific hosts are attacked by a common parasite.

C 22. If two or more species of specific hosts are attacked by a common parasite species, one of the hosts must completely displace the others, unless the properties of the hosts are identical.

This follows at once from C 2, and clearly that species of host capable of maintaining the density of the common parasite at the highest value must completely displace the other hosts, however slight its special advantage may be.

C 23. If the properties of the host species are identical, the steady density of the total of host species is equal to the steady density any one of them would maintain if it were alone attacked by the given species of parasite.

This is evident, for, when the individual hosts all have the same properties, it is immaterial whether they be considered to belong to one or to several species. The balance between the host species is clearly neutral, that is to say, any given fraction of the total hosts may consist of any one of the host species, and this fraction tends to be maintained from generation to generation. This situation is evidently of no more than theoretical interest, but its examination will assist us in subsequent investigations.

C 24. The effectiveness of a species of parasite in controlling the density of a particular host species at a low value is increased if the parasite also attacks other species of hosts.

This increased effectiveness may be represented by the area of discovery a *specific* parasite would require to possess in order to control the density of the host at the same value. This is referred to as the *equivalent area of discovery* of the given general parasite for the given host under the given conditions. Thus, let us suppose that equal numbers of two species of hosts, having identical properties, are attacked by a common parasite species. It follows from C 23 that the steady density of each of these hosts is half what it would be if the host were alone attacked by the given parasite. From C 6 it is clear that this is the effect that would be produced by a specific parasite with an area of discovery twice as great as that of the given common parasite, so the presence of the other host species has doubled the equivalent area of discovery of the common parasite for each of the hosts. Similarly, if the common parasite destroys twice as many individuals of one of the species (A) as of the other (B), then the steady density of A is two-thirds, and that of B one-third, of what it would be if the host (A or B) were alone attacked by the given parasite. Consequently the equivalent area of discovery of the given parasite for A is one

and a half times, and for B three times, its actual area of discovery. These and other similar numerical examples show that:

C 25. The equivalent area of discovery of a parasite species for a given host species varies inversely as that fraction of the total of attacked hosts which consists of hosts of the given species.

It should also be noticed that:

C 26. If a general parasite is caused to attack more hosts of one species, then fewer individuals of its other host species are available for attack, in the steady state.

This conclusion follows immediately from *C* 23, *C* 24 and *C* 25.

(*d*) *Several hosts and several parasites interact.*

This is the general problem of interacting hosts and parasites; any of the hosts and parasites may be specific or general, and they may interact in any conceivable combination.

C 27. For the steady state to exist, there must be at least as many parasite species as host species.

This follows from *C* 2, for the only control factors in the present situation are parasites, and so each host must possess an advantage over all other hosts with respect to at least one parasite.

C 28. When several species of general hosts are attacked by a common parasite species, balance may be established between them, even though their properties differ greatly.

When several species of specific hosts are attacked by a common parasite, one of them inevitably displaces the others (*C* 22), but when each species of host is also attacked by other parasite species, any tendency for one of the hosts to be displaced tends to cause a reduction in the severity of the attack of one or more of its other parasite species. Consequently, if the situation complies with *C* 2 and *C* 27, it should in general be possible for all the species of hosts to exist in the steady state, for each host may regulate the density of one or more of its parasites to its own requirements. However, the steady state is not inevitable, for it may happen that no possible reduction in the severity of the attack of those parasites that are regulated by the given species of host is sufficient to counterbalance the severity of the attack of a common parasite that is maintained by some other host species.

C 29. Balance between general parasite species that attack a common host species may be established even though the properties of the parasites differ greatly.

In the present situation the only control factors of the parasites are hosts, so (by *C* 2) each parasite must possess an advantage over all the other parasites with respect to some one, or group, of hosts. When a host is wholly controlled by a given parasite, this parasite clearly cannot be displaced, for the density of

the given host may always be adjusted to its requirements (see *C* 1). However, when a parasite is controlled by hosts that are partly under the control of other parasites, balance is likely but not inevitable. Thus, when the severity of the action of other parasites tends to displace the given parasite from a common host, other species of hosts that are partly under the control of the given parasite tend to increase (cf. *C* 26), and so tend to counteract the displacement of the given parasite. But the degree to which the given parasite may regulate the density of its hosts to its own requirements is here limited, and so the reaction of the hosts it partially controls may not be sufficient to prevent the displacement of the parasite.

C 30. The equivalent areas of discovery of general parasite species that attack a common host species automatically reach the values necessary for balance.

This gives the mechanism of *C* 29. Let us suppose that two general parasite species attack a common host species, and that one of them (*A*) is in process of displacing the other (*B*). This is the situation that would exist if the parasites were specific and the area of discovery of *B* were relatively too low to permit of balance with *A*, so the equivalent area of discovery (see discussion of *C* 24) of *B* is temporarily too low to permit of balance with *A*. But the discussion of *C* 29 shows that as *A* reduces the number of individuals of the given host species available to *B*, other host species available to *B* tend to increase. Consequently the equivalent area of discovery of *B* for the given host progressively increases (*C* 25) and would become indefinitely large if *B* were caused to attack a very small number of hosts of the given species. Before this extreme could be reached the equivalent area of discovery of *B* is bound to attain a sufficient value to permit of balance with *A*, when the tendency for the displacement of *B* would be arrested. However, if *B* does not wholly control the density of any one of its hosts the reaction of the hosts other than the given one may not be as just described, and so the equivalent area of discovery of *B* for the given host may never reach the value required for balance. If so, *B* ultimately vanishes. This can happen only with species that do not comply with the conditions of *C* 1.

C 31. An increase in the area of discovery of a parasite species for a given host species may decrease the steady density of the parasite or leave it unchanged.

The steady density of the parasite may be (1) independent of, (2) wholly dependent on, or (3) partly dependent on the density of the host for which its area of discovery is increased. Clearly in situation (1) the density of the parasite is unchanged, and in situation (2) the density is decreased (*C* 6 and *C* 15). Situation (3) is intermediate between (1) and (2), so the density of the parasite might reasonably be expected to be generally decreased, but there is reason to believe that under certain circumstances it may be increased.

C 32. An increase in the area of discovery of a parasite species for a given host species may either increase or decrease the steady density of the host at any given stage of its life cycle.

It has already been shown that increase in the area of discovery of any one of several specific parasites that attack a common host decreases the density of hosts at the stage attacked by the given parasite (*C* 14), while the initial and final steady densities are equally as likely to be increased as decreased.

Now let us examine a situation identical with that just considered except that the density of the given parasite is uninfluenced by the given host (e.g. because it also attacks a specific host for which its area of discovery remains unaltered). Clearly, when the area of discovery of the given parasite is increased for the given host, this parasite will attack a larger fraction of the surplus hosts of the given species than before. Consequently it will behave like a *specific* parasite with a *decreased* area of discovery (*C* 14), and its equivalent area of discovery for the given host will therefore be decreased (*C* 30). So, in the present situation the increased area of discovery of the given parasite causes a decrease in the host density wherever it caused an increase in the preceding situation, and *vice versa*.

These examples show that whether the density of the given host at any particular stage is increased or decreased, by a given change in the properties of one of the animals, is determined by the nature of the interrelations of the animals. The same result is obtained when more complex situations (e.g. the interaction of general hosts and general parasites) are examined.

C 33. Raising the power of increase of a host species in general tends to increase the steady density of the host, but it may decrease the density at any stage in the life cycle, this being most probable at the final stage.

As a larger fraction of the host offspring is surplus, for the steady state to exist the parasites are required collectively to increase in density. If all the species of parasites attacking the given host species also attack hosts of other species, then any increase in the available density of the given host automatically tends to cause the parasites to reduce the density of their other hosts (cf. *C* 26). Consequently, the density of the given host must increase sufficiently, not only to support the required increased density of the parasites, but also to take the place of the reduction in the densities of the other hosts of the parasites. On the other hand, if the parasites of the given host are specific, the final steady density of the host is decreased, while the density of the host at any other stage may be either increased or decreased, according to the number of parasites in the series (*C* 19). Consequently, if general parasites are mainly under the control of the given species of host (i.e. almost specific), it is possible that the density of the host may be decreased at any stage, and particularly at the final stage.

C 34. General parasites and general hosts with widely different properties may interact and maintain balance, and this balance is unlikely to be destroyed

even by great modifications of the properties of any of the animals, or of those of the environment.

This follows from *C* 28–*C* 33, but the limitation of *C* 27 should be noticed.

C 35. The introduction of a new parasite species in general tends to reduce the steady density of the host species it attacks, but it may increase the density of the host, and, if it is a general parasite, it may exterminate the host.

This follows from *C* 33, for the successful introduction of a new parasite causes a smaller fraction of the surplus hosts to be destroyed by the original parasites, i.e. the effective power of increase of the host, with reference to the original parasites, is reduced. If the introduced parasite is a general one, attacking other species of hosts in the new country besides the one particularly considered, these other hosts may maintain its density at such a value that it destroys more than the surplus of the given host. If so, the given host is exterminated.

(*e*) *The influence of hyperparasites.*

C 36. In general, hyperparasites should produce little effect on the densities of hosts, though they tend to increase these densities.

Recognising that the fraction of parasites destroyed by true hyperparasites is generally small, this conclusion follows from *C* 6, so far as it applies to specific parasites and hosts. If, however, the host is also attacked by other species of parasites, the increase in its density, which tends to be produced as a result of the attack of the given species by hyperparasites, is likely to be modified by the action of these other parasite species. The attack of hyperparasites, as it reduces efficiency, is equivalent to reducing the area of discovery of the attacked parasite species; so it is seen from *C* 32 that the density of a host may even be decreased, when one of the species of parasites that attack it is in turn attacked by hyperparasites.

However, if a hyperparasite attacks a certain species of parasite more efficiently than this parasite attacks its host, the hyperparasite destroys the whole of the surplus offspring produced by the parasite, and maintains the density of the parasite below that necessary to destroy the surplus of hosts. Consequently the hyperparasite completely frees the host from the control of this parasite. This situation seems very improbable.

B. *Interspecific oscillation.*

So far we have confined attention to the steady densities of interacting hosts and parasites. It is now necessary to consider whether there is anything to cause the interacting animals to reach, and to maintain, these densities.

A little thought shows that any departure from the steady density sets up a reaction that *tends* to cause a return to this density. Thus an increase in the density of the parasites causes them to destroy more than the surplus of hosts, so reducing the density of hosts in the next generation, and this in its turn

reduces the density of parasites. Similarly, an increase in the density of hosts causes the parasites to produce more offspring, and this increase in the density of parasites causes them to destroy more than the surplus of hosts. So any departure from the steady density sets up a reaction that tends to cause a return to this density, but there is always a delay in the appearance of the reaction.

Now let us suppose that the density of a host is above its steady value and is in process of being reduced by some species of parasite. When the host reaches its steady density, the density of the parasite is a result of the host density in the *preceding* generation, when it was above the steady value. Consequently there are more than sufficient parasites to destroy the surplus hosts, so the host density is still further reduced in the following generation. This is a new displacement from the steady density of the host, in the opposite direction to the original one. Consequently it sets up new reactions, of opposite sign to the original ones. Clearly, then, the densities of the interacting animals should oscillate about their steady values.

In order to investigate the character of such interspecific oscillation it is necessary either to use mathematics or to examine special numerical examples. For the present, attention is confined to the latter method.

C 37. When a specific parasite and a specific host interact, an oscillation in the densities of the animals about their steady values is produced, and this increases in amplitude with time.

This conclusion is illustrated by Fig. 6 for a particular numerical example. Further investigation and other numerical examples show that, when a specific parasite and a specific host interact:

C 38. Interspecific oscillation is independent of the area of discovery of the parasite.

C 39. The greater the power of increase of the host, the greater is the violence of interspecific oscillation, and the shorter is the period of oscillation, the minimum period being four generations.

Comparison of Figs. 6 and 7 demonstrates this for particular numerical examples.

It is also found that when a species of host is attacked by several successive species of specific parasites, and when it is attacked by a specific parasite that is also attacked by a hyperparasite, the interspecific oscillation is of the same increasing type.

C 40. When interacting animals are subject to increasing oscillation, they tend to be maintained permanently at densities much below their steady values, the animals being irregularly distributed in small groups, the positions of which are continually changing.

In outline, the argument on which this conclusion is based is as follows. With increasing oscillation the densities of the interacting animals must sooner or later be reduced to very low values. In the next generation it is clear that

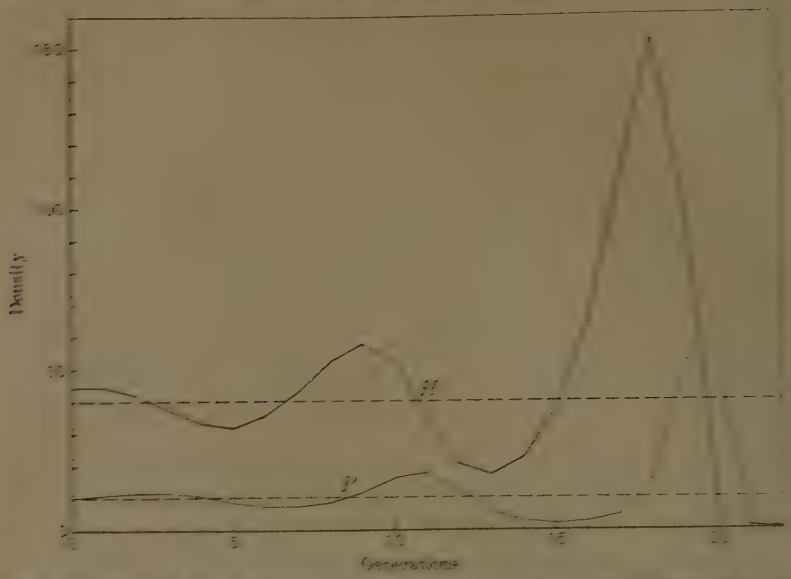


Fig. 6. Interaction of a specific host species H and a specific parasite species P. P was introduced at host 2. Area of discovery of parasite 0.02. Arbitrary initial displacement of host density from 100 to 44. H, host curve. P, parasite curve. The steady densities are represented by dotted lines. **Parasite curve drawn to half the vertical scale of host curve.**

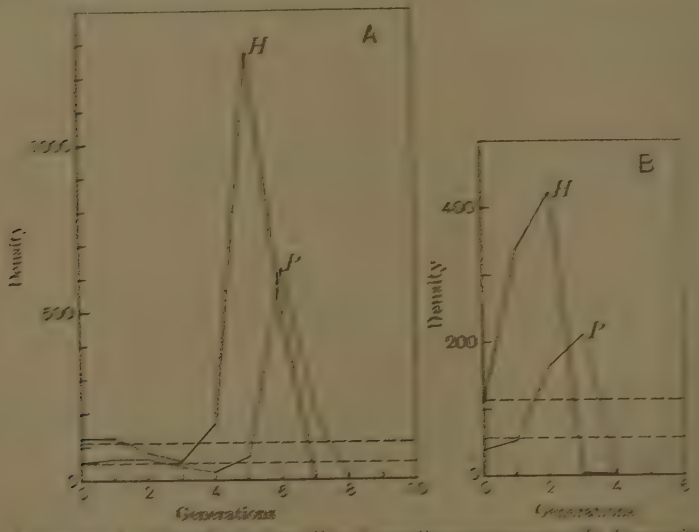


Fig. 7. Interaction of a specific host species H and a specific parasite species P. P was introduced at host 50. Area of discovery of parasite 0.005. Arbitrary initial displacement of host density from 114 to 128 in A. Arbitrary initial displacement of parasite density from 111.7 to 90 in B. **Parasite curve drawn to half the vertical scale of host curve.**

the animals must be scattered in the environment in more or less widely separated groups, for each female forms a centre from which its offspring diffuse. Some of these groups are found by parasites, and it is likely that these groups will be exterminated[1] during the next few generations, the course of events being similar to that shown in Fig. 7 B. The other groups of hosts increase geometrically for a few generations, but are sooner or later found by parasites and are ultimately exterminated; in the meantime there has been a migration of hosts, some of which have established new groups. Thus, instead of there being a simultaneous oscillation of the animals throughout the whole environment, there are large numbers of independent local systems of oscillation, all phases of oscillation being represented in the environment at any given time. The fact that parasites can develop only in areas in which hosts occur means that such areas are searched more intensively than the rest of the environment. Consequently, the parasites do not have to cover a fraction of the whole environment equal to the fraction of hosts that is surplus, but only need to cover a much smaller fraction in order to find the surplus hosts. Therefore the density of parasites, and consequently the density of hosts, necessary for balance under the given conditions is much below the calculated values of the steady densities of the animals.

C 41. When there is an upper limit to the density an animal may reach, interspecific oscillation may be maintained indefinitely.

When a species increases in density it impairs its environment, for example by reducing the amount of available food. Therefore it is possible that a host may be prevented from reaching a very high density which otherwise is permitted by its parasite. If so, the parasite cannot reduce the host to a very low density as a result of interspecific oscillation, for very low densities can be produced only as an effect of preceding very high densities. Therefore the scattering of animals in small groups that is produced at very low densities (see *C* 40) does not occur, and interspecific oscillation persists indefinitely, its amplitude remaining constant under constant conditions.

There is reason to suspect that the fluctuations in the numbers of soil organisms observed by Cutler, and referred to by Russell in the following passages, were interspecific oscillations of the present type. "One of the most striking properties of the soil population shown by all the groups for which examination is possible, is that the numbers do not remain constant, even under apparently constant conditions, but fluctuate continuously in number.... Bacteria did not fluctuate in numbers when grown by themselves in sterilised soil; they rose to high numbers and remained at approximately a constant level. Their numbers fell, however, as soon as the soil amoebae were introduced, but no constant level was reached; instead there were continuous fluctuations as in normal soils" (**19**, p. 331). "There is a sharp inverse relationship between

[1] Compared with a species population the number of individuals in a group is small, so at the minima of violent oscillations the groups of individuals are generally exterminated (see p. 143).

the numbers of bacteria and those of active amoebae; when the numbers of amoebae fall, those of the bacteria rise, and, conversely, when the numbers of amoebae rise, those of the bacteria fall" (**19**, p. 317).

C 42. When a parasite attacks other host species in addition to the one it controls, interspecific oscillation is reduced in violence and its amplitude is likely to decrease with time.

The violence of interspecific oscillation when specific hosts and parasites interact is clearly due to the powerful reaction of any one of the species to any departure of the density of the other from its steady value. However, when the controlled species is only one of several hosts a given species of parasite attacks, if the density of the controlled host is, say, doubled, this does not

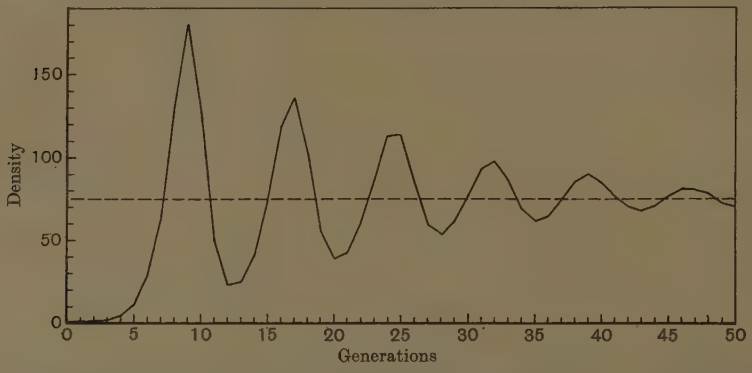


Fig. 8. Interaction of a specific host species and a general parasite species. Power of increase of host 10. Area of discovery of parasite 0·01. Steady density of specific host 75·5, and that of some other host of the given parasite 180. The density of the latter is independent of the activity of the given parasite and remains indefinitely at 180. Initially the given parasite is in equilibrium with this host and the specific host is introduced at a density of 0·1. Host density only is shown.

double the density of the parasite in the next generation; it only increases the density to some lesser degree, for the density of the parasite is also in part determined by its other hosts, the densities of which are controlled by other factors. Consequently, the violence of the reaction of the given parasite is reduced, and if this reduction is great it is evident that interspecific oscillation may decrease with time, rather than increase. Figs. 8 and 9 show that this is so. In Fig. 9 the controlled host has a smaller influence on the density of the given parasite than it has in Fig. 8. These figures, and the foregoing argument, show that:

C 43. The smaller the influence of the controlled host on the density of the parasite, the smaller is the oscillation.

It is of interest to note that the curve in Fig. 9 resembles the well-known form of a growth of population curve (see Pearl (**18**)). When the influence of the

controlled host on the given parasite is even less than in Fig. 9 the resemblance is very close.

The considerations given in this section show that:

C 44. Only when the parasites are not specific do the calculated steady densities correspond with those which animals actually tend to maintain.

However, there is reason to believe that the relative values of the densities specific parasites and their hosts tend to maintain should correspond to the relative values of their respective steady densities, but this correspondence may be modified if the various species have different powers of diffusion. It should also be noticed that under certain circumstances the densities of specific hosts and parasites are caused continually to oscillate about their respective steady values (*C* 41).

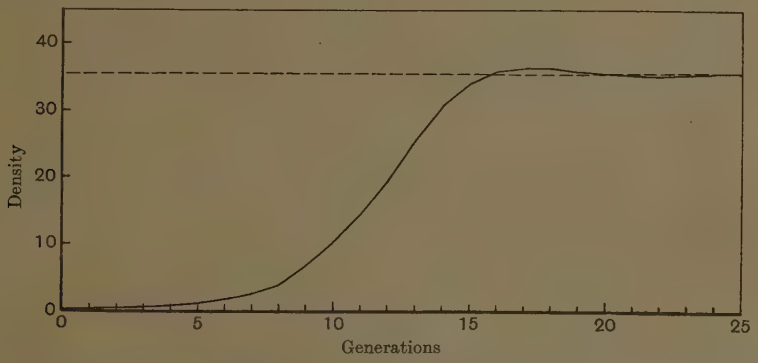


Fig. 9. Interaction of a specific host species and a general parasite species. Data as in Fig. 8, except that at equilibrium the specific host has a density of 35·5 and the other host a density of 220.

(3) THE INTERACTION OF PREDATORS AND PREY.

A. *The steady state.*

Parasites of the kind so far considered, i.e. entomophagous parasites, are actually predators of a special type, and their hosts are prey, for, unlike true parasites, these parasites destroy and consume their hosts. The mechanism of balance between true predators and their prey is essentially similar to that between such parasites and their hosts, for the predators destroy the surplus of hosts and the hosts support a density of predators necessary to do this. As a result, it is found that the conclusions reached by the investigation of the interaction of parasites and hosts apply in a general way to interacting predators and their prey, but need to be modified in detail. For the present it is sufficient to confine attention to certain features in which true predators differ markedly from entomophagous parasites. The most important difference

between parasites and predators is that, while the number of offspring produced by parasites is proportional to the number of hosts they find, there is no simple relation between the number of prey found by predators and the number of offspring they produce. All mature predators tend to produce a surplus of offspring, so it is clear that in the steady state this surplus must in some way be destroyed. Consequently:

C 45. The observed destruction of surplus predators does not indicate that the efficiency of a predator species is impaired.

It is generally recognised that in nature few animals die as a direct result of starvation. It is reasonable to believe then, that surplus predators are destroyed as an indirect effect of malnutrition, for predators can be controlled by their prey only if their chance of survival is influenced by their success in finding prey. Clearly, a half-starved predator should be more easily attacked than a fully vigorous one, and the observed fact that predators are commonly heavily attacked by other predators shows that this is a likely method of control. Also, it appears to be the only one that can cause the densities of predators to bear any relation to the densities of their prey. So:

C 46. The surplus of predators is destroyed by other predators as an indirect effect of difficulty in finding sufficient prey.

C 47. Cannibalism increases the efficiency of predators and enables them to maintain their prey at a lower density than would otherwise be possible.

When the surplus predators, instead of dying of starvation, are eaten by other predators of the same species, the survivors obtain at second-hand some of the nutriment provided by the prey that were eaten by the surplus predators. In other words, to the normal area of discovery of a surviving predator is added some fraction of the area of discovery of each of the surplus predators it eats. Thus the efficiency of the average surviving predator is increased by cannibalism, so permitting the steady density of predators to be maintained in a lower density of prey than would otherwise be possible.

C 48. The attack of primary predators by other species of primary predators tends to increase the efficiency of the predators in maintaining their own densities, and in controlling the densities of their prey at low values.

The surviving predators are collectively supported by the prey eaten by the attacked predators, as well as by the prey they themselves have eaten. Consequently the density of predators necessary to destroy the surplus of hosts can be supported in a lower density of prey than would otherwise be possible. The predator species share this advantage between them.

C 49. The attack of predators by special natural enemies may either increase or decrease the efficiency of the predators, but in general produces little effect.

If special natural enemies of primary predators attack these when very young, they decrease the intensity of competition between the survivors, so increasing the efficiency of the primary predators in controlling their prey. If

the special natural enemies attack primary predators when almost mature, the steady density of primary prey must be increased, for the prey are required to support to maturity those predators that are ultimately destroyed by natural enemies as well as those that ultimately reproduce. In general, the effect of special natural enemies is to destroy some of the surplus primary predators that in any case must be destroyed, so they only reduce the efficiency of primary predators in that they prevent these predators from enjoying to the full the benefits of cannibalism (*C* 47 and *C* 48).

C 50. It is possible that special natural enemies may prevent primary predators from controlling the densities of their prey.

If special natural enemies can control predators at a lower density than that necessary for the destruction of the surplus primary prey, the prey are completely freed from the control of the given predators and their density progressively increases until arrested by some new factor.

B. *Interspecific oscillation.*

C 51. The interspecific oscillation of predators and prey should in general be less violent than that of parasites and hosts.

In contrast to parasites, predators present the following features. (1) Their offspring commence to search shortly after they are born, so a variation in the number of offspring produced by predators causes an almost immediate variation in the intensity of attack delivered against the prey. (2) Predators deliver an increased severity of attack in the same generation in which an increase in the density of prey takes place, for fewer predators then die as a result of difficulty in finding prey. (3) The attack of predators by other primary predators permits more predators to survive when prey are scarce than would otherwise be possible (*C* 47 and *C* 48). (4) When the density of prey increases above normal, this does not cause a corresponding increase in the number of offspring produced by predator individuals (see p. 166). (5) An increase in the density of prey increases the density of surviving predators, so, though individually these may produce no more offspring than usual, the total number of offspring produced in the predator population may be considerably increased.

It will be observed that, in comparison with parasites and hosts, (1) and (2) reduce the delay in the production of reactions, (3) and (4) reduce the intensity of the reactions of predator densities to variations in the densities of prey, while (5) shows that an increase in the density of prey causes a subsequent increase in the density of predators. Thus the conditions necessary for the production of interspecific oscillation exist, but the lesser delay and intensity of the reactions should reduce the violence of oscillation (see *C* 42). It may therefore be concluded that:

C 52. In general, predators and their prey should tend to be maintained at their steady densities, for increasing oscillation is unlikely to be produced between predators and prey.

(4) Competition between animals for suitable location and food.

The precise places in which the habitats of animals exist, i.e. where all conditions are suitable for the existence of animals, are here referred to as *suitable locations*. Also, the word *food* is here used in a restricted sense that does not include hosts and prey, for we are now concerned with the competition of animals when searching for objects which, unlike hosts and prey, are *produced* in quantities that are entirely independent of the activities of the searching animals.

C 53. The minimum density of suitable locations necessary for the existence of a species varies inversely as the area of discovery, and also tends to vary inversely as the power of increase, of the species.

If inability to find suitable locations causes exactly the surplus of animals to be destroyed when there is no competition, i.e. when the density of the given species is indefinitely small, it is clear that the density of suitable locations has then the minimum permissible value for the existence of the given species. If the area of discovery is, say, doubled, the minimum permissible density of suitable locations is halved, for only thus can exactly the surplus of animals be destroyed without competition. If the power of increase is, say, doubled, the fraction of animals required to survive in the steady state is halved, and this should be supported if the minimum permissible density of suitable locations is also halved. However, more detailed investigation shows that this is only approximately true, for the fraction of its area of discovery traversed by an average animal before coming to rest in a suitable location varies with the fraction of animals that succeed in finding suitable locations.

C 54. Before all suitable locations are occupied, the densities of animals are limited by difficulty in finding unoccupied ones.

Balance is reached when difficulty in finding suitable locations, plus the intensity of competition, causes the destruction of exactly the surplus of animals. In Fig. 10 is shown the fraction of suitable locations occupied in the steady state when the density of suitable locations has any given value (measured in terms of the lowest permissible value). It is clear from this that animals should occupy almost the whole of the available suitable locations unless the power of increase is very low or the density of suitable locations is less than about four times the lowest permissible value. However, as the density of suitable locations is independent of the activity of the searching animals, it is likely at times to approach the lowest permissible value. Consequently, even when animals are controlled by the availability of suitable locations, they must be expected sometimes to leave many suitable locations unoccupied.

C 55. When food is continually produced, the density of animals is independent of, and the density of food always present is inversely proportional to, the area of discovery of the animals.

In the steady state there can be only one density of animals, namely, that at which food is consumed at the rate at which it is produced. If, then, the area of discovery is, say, doubled, the density of animals is unaltered, while the amount of food existing at any moment in the environment is halved, for the animals hunt for food twice as quickly as before.

C 56. The density of food always present is independent of the rate of production of food.

If the rate of production of food is, say, doubled, the density of animals is also doubled (see *C* 55) and so the food is found twice as quickly as before. Consequently, the amount of food existing in the environment at any moment is unaltered.

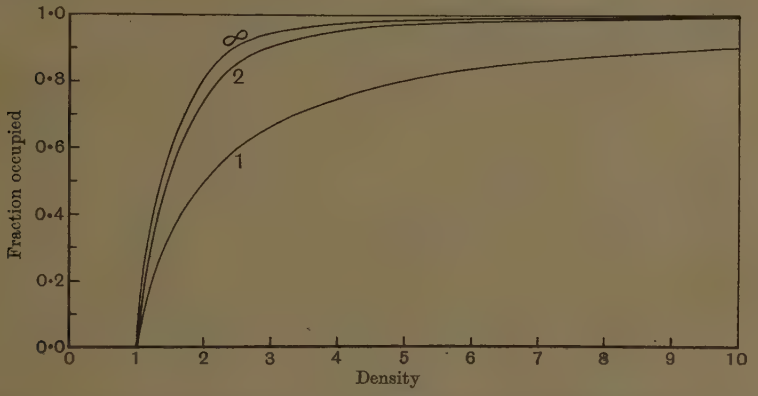


Fig. 10. Curves showing the fraction of suitable locations occupied in the steady state when the density of suitable locations has any given value up to 10, the lowest permissible density being the unit of measurement. The curves are for animals respectively having powers of increase of infinity, 2 and 1.

C 57. The density of animals is proportional to the amount of food produced in the lifetime of an animal.

For the steady state, food must be consumed at the rate it is produced. Assuming that the amount of food consumed per animal is constant, if its lifetime is, say, doubled, an animal consumes food at half the rate, and so double the density of animals is required to consume food at the rate it is produced.

C 53–*C* 57 are strictly true only on the following assumptions: (1) there is a continuous and constant generation of animals; (2) the surplus animals do not find any food; (3) the food always remains suitable for consumption by the animals. If these assumptions are not made the conclusions need to be modified, but in general character they remain true.

C 58. If the food ceases to be edible after it has been exposed for a certain period, there is a lower limit to the rate of production of food for any given species of animal, at less than which the species cannot exist.

If no animals operate there is clearly a limited density of food remaining edible at all times. If this density is such that, in the absence of competition, more than the surplus of animals fail to find food, the species clearly cannot exist.

C 59. Even though the density of a species is wholly controlled by the availability of food, in the steady state there must always be some food remaining unattacked in the environment.

Only if no time elapsed between the production of food and its discovery and consumption by animals could this be untrue. So animals must not be expected to increase in density until all food is consumed.

C 60. The control of the densities of animals by the availability of food is consistent with the observed fact that few animals die as a direct result of starvation.

As an indirect effect of difficulty in finding food the surplus animals are likely to be destroyed by natural enemies (cp. *C* 46) or adverse weather conditions, while the discovery of insufficient food may lower the birthrate of animals.

C 61. If there are fluctuations in the rate of production of food, the densities of animals fluctuate in relation to these, with some delay; and the quantity of food existing in the environment is not maintained by the animals at an absolutely constant value, but fluctuates in fairly close relation to the fluctuations in the rate of food production.

The density of animals continually tends to reach that necessary for balance with the rate of food production (*C* 57) and so fluctuates, but the nature of the reactions of the animals does not permit of precise correspondence between the fluctuations of food and of animals, so here the relation necessary for *C* 56 does not exist.

C 62. When animals are controlled by the availability of food there is little tendency to produce oscillations in density, and the densities should strongly tend to remain at their steady values.

If the density of animals is above the steady value there is an almost immediate reduction in the density of food and, in turn, an almost immediate decrease in the density of animals. Similarly, if the density of animals is too low, there is an almost immediate increase in the density of food, and so of surviving animals. As interspecific oscillation is primarily dependent on the delay in the production of reactions (see p. 161), there is little likelihood that animals controlled by the availability of food should oscillate in density.

(5) The influence of animal behaviour on populations.

One type of behaviour has already been considered and it has been shown (p. 141) that, so long as animals, or groups of animals, search independently, the searching within a population must be random. This remains true, however systematically the individual animals (or groups of animals) may search.

Systematic searching by individuals increases the areas of discovery of animals to some extent, but does not otherwise influence populations.

C 63. The territory habit produces a stable equilibrium of the population density.

When animals lay claim to territories (see Howard (**10**), and Elton (**6**)), it is clear that in any given area there is room for only a limited number of territories. Consequently the surplus individuals are continually harried by their more fortunate brethren, or are forced into unsuitable environments, and so their chance of survival, and of producing offspring, is greatly reduced. The system of balance resembles that of water in an overflowing reservoir; and there is no tendency to produce oscillations in density. If the animals having territories are natural enemies, they clearly tend to destroy a constant absolute number of prey. Consequently the fraction of prey they destroy tends to vary inversely as the density of prey, so the territory habit tends to make natural enemies behave in the opposite way to control factors (see Strickland (**20**)).

C 64. Certain predators (e.g. birds) tend to concentrate attention upon those parts of the environment in which prey are abundant, and so tend to damp fluctuations in the densities of their prey.

Many predators have two modes of locomotion (e.g. flight and hopping, or running and creeping), one of which is used in a cursory random survey of the environment for aggregations of prey or suitable places in which prey might occur, while the other is used for a slower and more detailed random survey of places in which prey are likely to occur. As different species of prey have different habitats they commonly occur in different places, so at any time the more abundant species are likely to be particularly heavily attacked by predators of the present type. This tends to damp any fluctuations in the densities of the prey, and also provides a mechanism by which a single species of predator may simultaneously control the densities of a number of different species of prey, for each species of prey tends to reach such a density that this causes the predators to destroy its surplus numbers.

C 65. When natural enemies in times of scarcity will attack prey other than the preferred species, this tends to damp the oscillation of the density of the preferred species.

Clearly a reduction in the density of the preferred species does not cause a corresponding reduction in the density of the natural enemies. The intensity of the reaction of the natural enemies being reduced, the violence of interspecific oscillation should also be reduced.

C 66. The polyphagous habit appears to be an almost essential adaptation of large natural enemies in order that the disadvantage of great size may be counterbalanced.

On the average, in traversing a given distance an animal must find sufficient food to provide the energy necessary for traversing that distance. Also, a large animal expends more energy, and so must find more food, than a small one when traversing a given distance. Small natural enemies tend to control the densities of their prey at the low values that are sufficient for their requirements, so, if large natural enemies are to exist in the same environments as small ones, they must be able to utilise more sources of food than the small natural enemies. However, this is not necessarily true if the large natural enemies are much more efficient in finding and attacking prey than the small ones, or if the large natural enemies can attack species of large prey that are unavailable to the small natural enemies.

(6) The influence of the physical environment on populations.

C 67. The distribution and densities of all animals are ultimately dependent upon the physical environment.

The physical environment ultimately limits the distribution of all plants. Natural enemies are dependent upon their prey and these, in their turn, upon their food plants. Consequently, the organisms with which given species of animals interact, and so the densities of the species, are ultimately determined by the physical environment.

C 68. Physical factors that are uninfluenced by the densities of animals cannot directly determine these densities.

Arguments supporting this conclusion have already been given (pp. 134–37). However, there are certain exceptional situations in which animals, like plants and micro-organisms, modify the physical nature of their environments. When this happens the densities of animals may be controlled by the reactions of physical factors, but even these are effects of competition (p. 140).

C 69. Physical factors may indirectly influence the densities of animals by modifying the positions at which other factors produce balance between animals and their environments.

Climate, in particular, may influence the vitality and activity of animals, so modifying the values of the powers of increase and areas of discovery, and consequently the steady densities, of animals.

C 70. The destructive action of physical factors may either increase or decrease the steady densities of animals.

This follows at once from *C* 9, *C* 19 and *C* 33, for when some fraction of the surplus hosts is destroyed by physical factors, the effective power of increase of the host with reference to its parasites is reduced. This conclusion applies when the physical factors are normal ones that operate continuously or periodically. An abnormal destructive factor inevitably reduces the density of a species as a direct and immediate effect, but if such a factor continues to

operate for a sufficiently long period its indirect effects may counteract or reverse the direct effects it tends to produce.

C 71. Migration, provided it is dependent upon the severity of competition, may control the densities of animals against which physical factors alone operate.

Competition forces the surplus animals into unsuitable portions of the environment, where they are destroyed by the physical factors (see p. 139).

C 72. Climatic oscillation causes interspecific oscillation of the decreasing type to be maintained indefinitely.

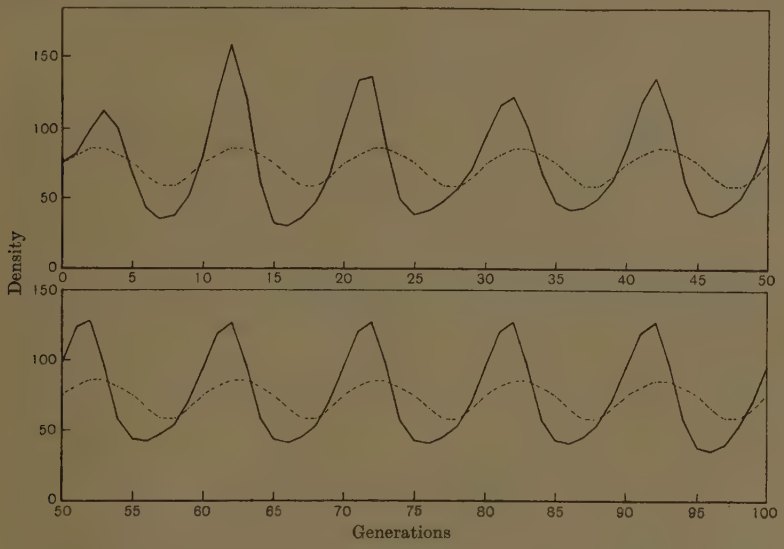


Fig. 11. Interaction of a specific host species and a general parasite species when under the influence of fluctuating climatic conditions. Data as in Fig. 8, except that the animals commence to operate in a state of equilibrium and, as an effect of climate, the power of increase of the specific host species changes in the following regular sequence: 10, 11, 12, 12, 11, 10, 9, 8, 8, 9, 10, and so on. Dotted line shows the steady density, and solid line the actual density of specific host species.

Fig. 11 and Figs. 8 and 9 are based on similar data, except that for Fig. 11 it is assumed that the value of the power of increase of the host periodically changes in relation to some periodic climatic change. In Fig. 11 the interacting animals start in a state of equilibrium, but subsequent variations of the power of increase of the given host cause a departure from the steady state. For about the first fifty generations the oscillations of the host density vary in amplitude but subsequently reach a particular amplitude which is maintained indefinitely under the influence of the given constant climatic oscillation. Thus the interspecific oscillation, instead of dying out as it does in Fig. 8, is indefinitely main-

tained, and this is due to the fact that fluctuating climatic conditions continually apply a small external force to the oscillatory system.

C 73. Interspecific oscillation tends to take the period of climatic oscillation that governs it.

This is shown by Fig. 11 and other similar examples that have been examined. However, when the periods of interspecific and of climatic oscillation are widely different this conclusion is no longer true.

C 74. Seasonal fluctuations in the densities of animals are more violent than one would expect from the known influence of climatic conditions on the properties of the interacting animals, and this violence is wholly due to the influence of interspecific oscillation.

The effects produced on the steady density of the host by climatic oscillation alone are shown by the dotted line in Fig. 11.

C 75. Irregular climatic fluctuations tend to produce closely associated irregular fluctuations in the densities of animals, but delayed effects cause further irregular fluctuations to be produced that have no apparent relation to climatic conditions.

The first six oscillations in Fig. 11 vary in amplitude, though they are all under the influence of precisely the same seasonal oscillation. Consequently, the amplitude is governed, not alone by the prevailing conditions, but also by the character of the preceding fluctuations. So a given abnormal climatic fluctuation not only influences the densities of animals subject to it, but also influences the densities of animals in subsequent generations. In addition, the resultant variation in the density of any given species causes subsequent variations in the densities of the species with which it interacts, and through these the impulses pass to all other species in the environment, with varying degrees of delay. This clearly should cause irregular fluctuations in the densities of animals that have no evident relation to variations in the physical environment.

C 76. Competition regulates the densities of animals in erratically and progressively changing environments just as it does in undisturbed environments.

Just as a cork moves in relation to the waves of a storm-tossed ocean only because it is in a state of balance on the surface of the water, so the densities of animals can vary in relation to variations in their environments only because competition is always tending to cause them to reach the position of balance corresponding to the prevailing conditions (see p. 135).

(7) Implications of the conclusions reached.

A. *Economic biological control.*

The significance of many of the conclusions already reached in the question of the utilisation of natural enemies to control pests is evident, and at present it is desired merely to mention certain points that are of particular importance to this question.

All species that are not progressively increasing in density are necessarily controlled; so the function of economic control is not to bring under control a pest that was previously uncontrolled, but to modify the control so that the density of the pest is reduced to a point at which the economic damage caused is negligible.

The importance of a factor in controlling a pest is not even suggested by the fraction of pests it destroys (p. 136). When searching for the control factors it is necessary to find which are influenced, and how readily they are influenced, by changes in the density of the pest (pp. 135 and 137).

Specific parasites, provided their life cycles conform closely with those of their hosts, should control pests at very low densities, the pests occurring in widely separated groups, the positions of which frequently change (*C* 40). General parasites should commonly control their hosts at higher densities than specific ones, the distribution of their hosts being fairly uniform (*C* 42), but, unlike specific parasites, a general parasite, when introduced, may exterminate a particular host (*C* 35). The effect produced on the density of a pest by the introduction of a new natural enemy depends not only upon the properties of this natural enemy, but also upon the nature of the complex of animals with which the pest originally interacted (*C* 18 and *C* 35).

It seems probable that the adverse influence of hyperparasites on the control of pests has been over-emphasised (*C* 36 and *C* 45–49), and that lack of success which has been attributed to the presence of hyperparasites was probably due to some other cause. However, it must not be forgotten that a hyperparasite may completely free a pest from the control of a particular natural enemy (*C* 36 and *C* 50).

B. *Natural selection.*

It has already been shown (p. 137) that natural selection not only cannot produce and preserve the "balance of nature," but must inevitably destroy the qualitative balance it is supposed to produce. Balance is produced and maintained by competition, not by natural selection.

When individuals having advantageous properties appear in a population, their chance of being amongst the survivors is greater than that of the normal individuals. In the course of time, then, the fraction of the population consisting of individuals with advantageous properties increases, so improving the average properties of the animals, and increasing the degree to which they overbalance the inherent resistance of the environment. But the severity of the action of intraspecific competition is automatically regulated to the requirements of each population (*C* 1). Thus the progressively increasing proportion of favoured to normal individuals causes a progressive increase in the severity of intraspecific competition. As the original degree of competition was sufficient to destroy the surplus normal individuals, the increased severity of competition must cause the destruction of more than the surplus of normal

individuals. Ultimately, therefore, the favoured type must completely displace the original normal type, though this would have remained successful indefinitely had the more favoured type not appeared.

Thus competition maintains balance in spite of the disturbing influence of natural selection, and adaptation that leads to the preservation of a type has nothing to do with a precise qualitative adjustment of its properties to those of the environment. Also, from *C* 31, *C* 32 and *C* 33, it is clear that the selection of a type with advantageous properties does not necessarily increase the density of the species. This and other arguments (see Nicholson (**17**)) show that natural selection operates without reference to the success of species. It simply favours those individuals that possess some advantage over their fellows, while leaving competition to determine the densities of the species and to maintain them in a state of balance with the environment.

SUMMARY.

1. The whole of this communication is essentially the summary of a much larger work, so it has been impossible here to do more than give an outline of its main features.

2. The densities of animal populations are known to bear a relation to the environmental conditions to which they are subject, and the existence of this relation shows that populations must be in a state of balance with their environments.

3. For balance, it is essential that the action of a controlling factor should be governed by the density of the population controlled, and competition seems to be the only factor that can be governed in this way.

4. Examination of the competition to which animals are subject shows that it is generally competition between animals when seeking the things they require for existence, or competition between natural enemies that hunt for them.

5. Detailed investigation of the question of competition between searching animals shows that, whether the animals are controlled by competition for food, or for suitable places in which to live, or by the competition of their natural enemies, there is for each species a particular density, referred to as the "steady density," at which balance exists. The value of this steady density depends upon the properties of the species, the properties of the species with which it interacts, the nature of this interaction, and the properties of the environment.

6. Competition always *tends* to cause animals to reach, and to maintain, their steady densities. Factors, such as climate and most kinds of animal behaviour, whose action is uninfluenced by the densities of animals, cannot themselves determine population densities, but they may have an important influence on the values at which competition maintains these densities.

7. When the densities of animals are controlled by natural enemies, this interaction itself produces oscillation, even in a constant environment. With

very simple types of interaction, such as that of a specific entomophagous parasite and its host, the oscillation of density increased in amplitude with time.

8. According to the circumstances, the final result of such oscillation is either the perpetual maintenance of the oscillation with constant amplitude under constant conditions, or the population is broken into widely separated small groups of individuals, the positions of which continually change with time. In the first situation the densities of the animals fluctuate about their steady values, but in the second the average densities are permanently maintained much below their steady values.

9. With more complex types of interaction the oscillation decreases in amplitude with time, so that in a constant environment the densities are caused eventually to reach, and to remain at, their steady values.

10. However, the environment does not remain constant, and it is found that periodic environmental changes, such as those of the seasons, tend to impress their period upon interspecific oscillation. Consequently the oscillation that is produced by the interaction of animals should generally be found to correspond in time with seasonal and other periodic environmental changes, but its violence is greater than that of the oscillation which these environmental changes could themselves produce.

11. Also, environmental oscillation applies an external force which prevents interspecific oscillation of the decreasing type from dying out. Irregular environmental fluctuations tend to cause corresponding irregular fluctuations in the densities of animals, but, owing to the delayed effects produced by interspecific oscillation, further irregularities in the densities of animals are subsequently produced that have no evident relation to environmental conditions.

ACKNOWLEDGMENTS.

I wish to express my great indebtedness to Prof. V. A. Bailey for the time and energy he has devoted to the mathematical investigation of the problems here presented. He has not only greatly increased the value of the work by giving rigorous proofs of the conclusions I had obtained by less precise methods, but has also extended the investigation to certain problems which could not be adequately investigated by the rather crude methods I had used.

The work on the present investigation has been lightened during the past few years by the interest and encouragement of my colleagues, originally at the Department of Zoology of the University of Sydney, and later at the Division of Economic Entomology of the Commonwealth Council for Scientific and Industrial Research, at Canberra, and I particularly wish to mention my indebtedness to Dr R. J. Tillyard, Mr G. A. Currie, Dr I. M. Mackerras and Dr P. D. F. Murray. I also wish to thank Prof. W. E. Agar and Prof. A. M. Carr-Saunders for their generous help and for the useful suggestions they made.

REFERENCES.

(1) **Bailey, V. A. (1931).** "The interaction between hosts and parasites." Q. J. Math. 2, 68–77.

(2) **Bodenheimer, F. S. (1928).** "Welche Faktoren regulieren die Individuenzahl einer Insektenart in der Natur?" Biol. Zbl. 48, 714–39.

(3) **Chapman, R. N. (1928).** "The quantitative analysis of environmental factors." Ecology, 9, 111–22.

(4) **Chapman, R. N. (1931).** "Animal ecology." New York and London.

(5) **Elton, C. (1930).** "Animal ecology and evolution." Oxford.

(6) **Elton, C. (1932).** "Territory among wood ants (*Formica rufa* L.) at Picket Hill." J. Animal Ecology, 1, 69–76.

(7) **Fisher, R. A. (1930).** "The genetical theory of natural selection." Oxford.

(8) **Fiske, W. F. (1910).** "Superparasitism: an important factor in the natural control of insects." J. Econ. Entom. 3, 88–97.

(9) **Holdaway, F. G. (1932).** "An experimental study of the growth of populations of the Flour Beetle, *Tribolium confusum* Duval, as affected by atmospheric moisture." Ecol. Monographs, 2, 262–304.

(10) **Howard, H. E. (1920).** "Territory in bird life." London.

(11) **Howard, L. O. and Fiske, W. F. (1912).** "The importation into the United States of the parasites of the gipsy-moth and the brown-tail moth." U.S. Dept. of Agric., Bureau of Entom., Bull. 91.

(12) **Lotka, J. A. (1920).** "Analytical note on certain rhythmic reactions in organic systems." Proc. Nat. Acad. Sci. 6, 410–15.

(13) **Lotka, J. A. (1925).** "Elements of physical biology." Baltimore.

(14) **Malthus, T. R.** "On the principle of population." London.

(15) **MacLagan, D. S. (1932).** "An ecological study of the 'Lucerne Flea' (*Smynthurus viridis* Linn.)." Bull. Ent. Res. 23, 101–45.

(16) **Martini, E. (1931).** "Zur Gradationslehre." Verh. Deuts. Ges. Angew. Ent., Mitglieder-Versamml. Rostock, Aug. 1930, 19–26. Berlin.

(17) **Nicholson, A. J. (1927).** "A new theory of mimicry in insects." Australian Zoologist, 5, Part 1. Sydney.

(18) **Pearl, R. (1926).** "The biology of population growth." London.

(19) **Russell, E. J. (1927).** "Soil conditions and plant growth." Rothamsted Monographs on Agricultural Science, London.

(20) **Strickland, E. H. (1928).** "Can birds hold injurious insects in check?" Scientific Monthly, 26, 48–56.

(21) **Thompson, W. R. (1924).** "La théorie mathématique de l'action des parasites entomophages et le facteur du hasard." Ann. Fac. Sci. Marseille, Ser. 2, 2, 69–89.

(22) **Thompson, W. R. (1930).** "The biological control of insect and plant pests." Publ. Empire Marketing Board 29, H.M. Stationery Office, London.

(23) **Uvarov, B. P. (1931).** "Insects and climate." Trans. Ent. Soc. London, 79, 1–247.

(24) **Volterra, V. (1926).** "Variazioni e fluttuazioni del numero d'individui in specie animali conviventi." Mem. Accad. Naz. Lincei (Sci. Fis. Mat. e Nat.), Ser. 6, 2, No. 3.

(25) **Volterra, V. (1927).** "Sulle fluttuazioni biologiche." Rend. R.A. dei Lincei, Ser. 6, 6.

(26) **Volterra, V. (1927).** "Leggi delle fluttuazioni biologiche." Rend. R.A. dei Lincei, Ser. 6, 6.

(27) **Volterra, V. (1927).** "Sulla periodicità delle fluttuazioni biologiche." Rend. R.A. dei Lincei, Ser. 6, 6.

(28) **Volterra, V. (1931).** "Leçons sur la théorie mathématique de la lutte pour la vie." Cahiers scientifiques, No. 7. Gauthier-Villars et Cie, Paris.